Carbon isotope discrimination by *Eucalyptus* species in the Northern Territory, Australia

Jeffrey M. Miller

A thesis submitted for the degree of
Doctor of Philosophy
at The Australian National University, Canberra, Australia

April 2002

The research described in this thesis is my own. I designed and was responsible for the experimental work myself. I have been solely responsible for the analysis of the data and its write-up. No part of this work has been submitted for a degree at any other University. The following papers derived in whole or in part from work presented in this thesis:

Miller, J.M., Williams, R.J. & Farquhar, G.D. (2001) Carbon isotope discrimination by a sequence of *Eucalyptus* species along a subcontinental rainfall gradient in Australia. Functional Ecology 15, 222-232.

Farquhar, G.D., Buckley, T.N. & Miller, J.M. (2002) Optimal stomatal control in relation to leaf area and nitrogen content. Silva Fennica 36, 625-637.

Buckley, T.N., Miller, J.M. & Farquhar, G.D. (2002) The mathematics of linked optimisation for water and nitrogen use in a canopy. Silva Fennica 36, 639-669.

31/01/2003

Jeffrey Miller Date

Acknowledgments

I would like to thank all the people who helped me with the research and production of the document that follows. First and foremost I would like to thank my supervisor, Graham Farquhar for accepting me as his student and providing the funding for this long and drawn out experience. I would also like to thank the other official and unofficial members of my supervisory committee, John Pate, Jim Virgona, John Evans, and Dick Williams.

In the field I was assisted by Jack Cusack, and Lins Vellen, and several Administrative Assistants of the Environmental Biology Group as well as Tom Buckley spent way more time than they should have printing the document.

I would finally like to thank Margi Bohm for the sacrifices she made during the time I was in Australia, none of which should have happened.

Summary

Carbon isotope discrimination (Δ) reflects the balance between the supply of CO_2 into the intercellular airspaces of a leaf and the demand of photosynthesis for CO_2 from those intercellular airspaces. The conductance of CO_2 into a leaf depends upon the plant being able to sustain the co-occurring transpiration, which requires the acquisition and transport of water at rates equal to the evaporative demand. The photosynthetic demand for CO_2 depends upon the investment of nutrients, primarily nitrogen, in photosynthetic enzymes. Plants with high conductance, relative to photosynthetic capacity, will have little reduction in intercellular CO_2 concentrations relative to the ambient source CO_2 concentration outside the leaf, and therefore high Δ values. Plants with either low conductances or high photosynthetic capacities will have low intercellular CO_2 concentrations and low Δ values, reflecting a high degree of stomatal limitation on photosynthesis. Carbon isotope discrimination therefore reflects the balance between the water and nutrient economies of plants, and when combined with information on the distribution of a species may yield insight into the success of the genetically determined growth strategy for the uptake and utilization of these resources.

From Darwin, on the north coast of Australia, to the southern border of the Northern Territory there is an eight-fold decrease in total annual rainfall with little topographic complexity. A transect across this gradient includes plant communities in the wetter northern areas that are dominated by *Eucalyptus* species, while the arid southern areas are dominated by potentially N-fixing *Acacia* species. This broad-scale replacement of a possibly high water-using growth strategy by a high nitrogen-using strategy along a gradient of decreasing water availability would seem ideal for study using carbon isotope discrimination. This is especially true since carbon isotope discrimination records a production-weighted measure of the ability of conductance to supply CO_2 for photosynthesis over time periods approximating the duration of the time required for the growth of the sampled tissue. The carbon isotope discrimination recorded in wood tissue would presumably record conditions over a full year in an annual growth increment, with conditions over many years being integrated by combining the growth during multiple years.

Although carbon isotope discrimination is a leaf-level phenomenon, it has been used as a successful surrogate measure of the water-use efficiency of co-occurring whole plants. Where the evaporative demands are the same, i.e. plants have similar leaf temperatures and therefore similar leaf-to-air vapor pressure deficits, and are not competing for the same limited water supply, slow rates of water-use (and necessarily limited rates of carbon gain) are more efficient, and will result in greater final biomass accumulation, than high rates of water use, assuming similar allocation patterns for reinvesting photosynthate towards resource acquisition. Low rates of water-use, and a high degree of stomatal limitation on CO_2 supply for photosynthesis will result in low Δ values correlating with this high biomass production. When any of those pre-conditions is not completely satisfied, arguments can be made that the plant with lower stomatal limitation on photosynthesis should be a better performer.

The ambiguity of the potential response of Δ to decreasing water availability in naturally occurring plant populations is work. Carbon isotope discrimination was measured in leaf and wood tissue across the distributions of a series of co-occurring and replacement species along a rainfall gradient. With decreasing rainfall, the whole-tissue leaf Δ of five of 13 species decreased, seven exhibited no trend, and one increased. The whole-tissue wood Δ of eight species decreased, showed no trend in four species, and increased in one species. Species replacements were marked by a shift in Δ reflecting greater stomatal limitation on assimilation. There was a non-linear response of the multi-species average leaf and wood Δ to decreasing total annual rainfall. This response reflected the spatial pattern of the sensitivities of Δ to decreasing rainfall of the individual species and was not the result of a proposed emergent behavior where the mean would differ from the responses of the individual species.

Because the patterns in Δ in response to decreasing water availability were not common to all species it was not possible to determine the extent to which Δ is a measure of the stomatal limitation on photosynthesis, i.e. is a measure of the reaction to environmental stress. The patterns of Δ across the distributions of the species did not provide a simple measure of the physiological limits of the distribution of eucalypts in northwestern Australia. As Δ measures the ratio of leaf conductance to assimilation capacity, movement in either factor could generate a signal, while combined movement could result in no signal.

Although the opportunity to directly measure the magnitude of leaf conductance and assimilation capacity in a subset of the sampling locations would have greatly assisted in the understanding of their dynamics across the transect and the patterns in Δ, assimilation capacity had to be estimated from leaf nitrogen contents. The increase in area-based leaf nitrogen contents is explored in Chapter 4.

The uptake of CO_2 can be viewed as a two-step process, the first involving CO_2

entering the leaf and stomatal conductance and the second involving the actual photosynthetic uptake from the intercellular airspace depending on leaf nitrogen contents and investment in photosynthetic enzymes. The two processes are in series such that a decrease in either could be offset by an increase in the other to maintain the overall photosynthetic rate. This principle of resource substitution is a basic idea of economics and there is a well developed mathematical treatment of the issue coming from the fields of consumer behavior and the production of firms. Such concepts as the intrinsic antagonism of water-use efficiency (the rate of carbon gain per unit water lost in transpiration) and nitrogen-use efficiency (the rate of carbon gain per unit nitrogen lost in leaf senescence) are obvious outcomes of resource substitution.

The mathematics of resource substitution and related concepts as applicable to a simple model of photosynthesis, transpiration, and root investment for acquiring water and nitrogen is developed in Chapter 4. The measured increases in leaf nitrogen contents were estimated to account for between 50 and 75% of the projected change in water-use as water availability decreased across the transect.

The increasing leaf nitrogen contents with decreasing rainfall across the transect were predicted to result in increased photosynthetic capacities. As water availability decreased there was also an increase in the leaf-mass per unit area and the leaf-carbon content per unit area. This increased investment of carbon in leaves was presumed to be a mechanism to withstand low water potentials and would result in longer periods to recover the costs of the leaves. From the calculated gas exchange rates (based on leaf nitrogen contents and leaf Δ) the patterns in the leaf payback period are predicted in Chapter 5. The predicted increases in photosynthetic capacities as a result of increases in leaf nitrogen contents were not large enough to balance the increases in leaf carbon contents, and all but one species was predicted to have increasing leaf payback periods with decreasing rainfall across their distribution. This increase in the time required to recover the cost of the leaves, combined with a predicted decrease in the maximum supportable leaf area index could indicate the physiological limits to the distribution of each species.

The environmental influences of decreasing water supply and increasing evaporative demand on leaf conductance are relatively well understood from experiments in controlled conditions (see Chapter 6). The link between leaf nitrogen contents and photosynthetic capacity, and then the theory relating Δ to leaf conductance and assimilation capacity are also well understood. The extent to which these links could be found in the 1300 measurements of leaf or wood Δ is explored in Chapter 6. Long-term predicted mean meteorological conditions did not explain the patterns or variability in leaf or wood Δ in a satisfying manner. The rainfall in the Northern Territory is strongly seasonal, so that the gradient in annual rainfall masks the fact that all along the transect there is a dry season with little or no rainfall for around three months or longer. The mean interval between rain events, or drought length, was often as important as rainfall in explaining patterns of Δ. This could indicate that selection has tuned the rate of water-use to match the time period between supply events.

The degree to which the trees of the Northern Territory are able to tap a reliable ground-water supply by increasing their allocation to root growth, and the degree to which they operate with partially open stomata (which would generate a low Δ signal) rather than merely operating in an open or shut mode (with would avoid recording a low Δ signal as there would be no concurrent assimilation) were beyond the scope of Chapter 7 which addressed the ability of the species to change their physiological and morphological characteristics across their distributions. Plasticity would allow a species to adjust to varying conditions, but is thought to be a risky behavior under the most extreme conditions when genetically controlled conservative behavior is often observed. Variability within populations may also decrease with increasing stress levels where only a limited sub-population of growth strategies remain viable. Physiological parameters, specifically wood and leaf Δ, had lower elasticities than the measured morphological parameters, emphasizing that subtle changes in Δ are of potentially great importance as indicators of plant performance.

Although carbon isotope discrimination should have allowed a quick and efficient method for broadly establishing the potential ecophysiological controls on the distributions of *Eucalyptus* species in the Northern Territory, to be followed upon by direct measures of gas exchange parameters, the realities of the method preclude its viability in the limited duration of a PhD thesis. No single measure conducted in a laboratory thousands of kilometers from the field can compensate for a lack of direct field experience.

Table of contents

Chapter 1

Carbon isotope discrimination, plant physiological performance, and the environmental controls on the distribution of species

1.1 Introduction

Continental scale environmental controls on species distributions have usually been inferred from the correlations of species presence and climate data. Direct measures of plant performance along environmental gradients are usually limited to simple growth measurements that do not provide insight into the underlying physiological characteristics that allow survival. An understanding of these mechanisms, and their responses under changing environmental conditions, will become necessary if we wish to insure their continuance in an increasingly anthropogenically dominated world. The physiological responses of species across their distribution along stress gradients, and the responses of a series of species which replace each other along a stress gradient are difficult to measure. Most measures of physiological parameters are spot samples in both time and space, and getting either long time-scale signals, or simultaneous signals at multiple locations requires indirect methods such as simulation modeling.

Australia is a unique continent for the study of ecophysiological controls on plant distribution. There have been long periods since Gondwana with stable land forms and a seasonal wet-dry climate (Pole & Bowman 1996), allowing the distributional equilibria of plant species to be reached. The lack of significant topographic variation reduces the micro-site complexity (e.g. Ehleringer & Cooper 1988).

Savannas, such as those of northern Australia, are the result of interactions between plant-available moisture and plant-available nutrients, with fire and herbivores also playing roles (Skarpe 1992). Total annual rainfall, and the length of the annual drought usually place savannas between deserts and dry-deciduous forests, but Australia is uniquely dominated by evergreen *Eucalyptus* species grading into evergreen *Acacia* species in the drier center (Walter 1973; Wilson et al. 1990). Resource substitution may explain this pattern, with *Acacias* having high water-use efficiency as a result of high leaf nitrogen concentrations, and therefore low nitrogen-use efficiency. There are large areas of relatively undisturbed native vegetation, especially in the north and central areas, that allow the study of climatic controls on the distribution of species without major anthropogenic disturbances (Williams et al. 1996). The understory in the area is, however, burned regularly and grazed by cattle which will indirectly affect the overstory (Andersen et al. 1998). Managed fires in the early dry season have the least impact on overstory survival, while late season fires following just 2-3 years of fuel build-up can kill up to 70% of the trees (Williams et al. 1999).

Across the Northern Territory there is a strong rainfall gradient, from around 1600 mm yr^{-1} in the north to around 200 mm yr^{-1} in the south, without the complication of large changes in elevation and temperature. The rainfall is strongly seasonal, with at least 4 months when there is practically no rain anywhere, so the gradient from the north to the south has a suite of covaring parameters; total annual rainfall, length of the annual drought, length of droughts in the wet season, evaporative demand, etc.

The vegetation varies in structure from open forest in the north to low open woodlands in the south (Wilson et al. 1990). The overstory is composed of equal numbers of species which are evergreen, brevi-deciduous, semi-deciduous, and deciduous (Williams et al. 1997). Many of the dominant *Eucalyptus* species show bands of distribution perpendicular to the rainfall gradient (Chippendale & Wolf 1981; Brooker & Kleinig 1994). Therefore the large continental scale patterns of species distributions could be linked to rainfall and physiological determinants of water-use efficiency.

Carbon isotope discrimination recorded in various plant tissues provides a method to investigate the physiological status of a plant when the tissues were created. By sampling tissues such as leaves which are grown in a narrow, “benign” season, and then wood which summarizes the full annual production weighted performance, two indicators of response are parameterized.

Leaf Δ reflects the internal partial pressures of CO_2 within the leaf (p_i), probably during a limited, sub-annual period when the leaves are formed (Farquhar, O'Leary & Berry 1982; Walcroft et al. 1997). The whole tissue value reflects some initial translocation of carbon into leaf before growth is self-generating, and includes a variety of secondary compounds with discriminations after the initial signal recorded in photosynthetic sugar synthesis.

Bulked wood Δ represents an unknown number of years annual production weighted signal. Trunk growth, which is possibly seasonal, may reflect current carbon during the period of greatest expansion, or the carbon may come from a storage reserve. Currently produced sugars will be converted to cellulose with a similar isotopic composition, but other sources of carbon may have fractionations along the full pathway. Other materials besides cellulose in the whole wood samples will have fractions following the initial signal during photosynthesis. The wood Δ will therefore be a "long-term signal" when compared to the leaves.

By measuring the carbon isotope composition ($\delta^{13}C$; ‰) and calculating the carbon isotope discrimination (Δ; ‰) it is possible to investigate the balance between the water and nitrogen economies of a species with the appropriate time and spatial scale data. Elemental analysis can quickly give values for the nitrogen and carbon contents of tissue, and an estimate of net photosynthetic capacity can be calculated from leaf nitrogen concentrations and specific leaf area (Reich, Ellsworth & Walters 1998). Knowing the assimilation rate and the carbon isotope discrimination allows an estimate of leaf conductance to be calculated, which when combined with estimated values of vapor pressure deficits generates an estimate of transpiration. An estimate of water-use efficiency can then be calculated, as can the potential maximum leaf area index (based on the total annual rainfall and plant water-use per unit leaf area). From the carbon content of the leaf tissue and the assimilation rate an estimate of the time required for the leaves to recover their construction costs is available. These characteristics, and the changes in these characteristics across the distribution of a species and with species replacements along an environmental gradient, begin to define the physiological mechanisms necessary for plant survival.

1.2 Carbon isotope discrimination and the balance between photosynthesis and conductance

The δ^{13}C of plant tissues reveal the Δ that occurred when the tissues were created, since

$$\Delta = \frac{\delta^{13}C_{\mathrm{air}} - \delta^{13}C_{\mathrm{plant}}}{1 + \delta^{13}C_{\mathrm{plant}}} \qquad \text{Eq. 1.1}$$

(Farquhar & Richards 1984). Discrimination against the heavier $^{13}CO_2$ during photosynthesis occurs during the diffusion of CO_2 through the stomata (a; 4.4‰), and during the carboxylation of CO_2 by ribulose bisphosphate carboxylase-oxygenase (Rubisco) (b; which is ~27.0‰ when the fractionations due to the movement of CO_2 from the intercellular airspaces, p_{i}, to the sites of carboxylation, p_{c}, are combined); summarized by Farquhar, O'Leary & Berry (1982) as

$$\Delta = a + (b - a)\frac{p_{\mathrm{i}}}{p_{\mathrm{a}}} \qquad \text{Eq. 1.2}$$

where p_{a} is the partial pressure of CO_2 in the ambient air. The ratio of p_{i} to p_{a} depends on the supply of CO_2 into the intercellular air spaces in the leaves ($g/1.6$; where g is the conductance to water vapor) and the rate of removal of CO_2 by photosynthesis (A), according to the rearranged standard supply equation for photosynthesis as

$$\frac{p_{\mathrm{i}}}{p_{\mathrm{a}}} = 1 - \frac{1.6\,AP}{g\,p_{\mathrm{a}}} \qquad \text{Eq. 1.3}$$

where P is the total atmospheric pressure. Carbon isotope discrimination therefore reflects the balance between conductance and assimilation, and this depends on the ability to keep the stomata open, and on the nitrogen investment in Rubisco (Evans 1989; Condon, Richards & Farquhar 1992).

The ability to maintain leaf conductance depends on the ability to acquire water from the soil and transport it through the tissues at a rate equal to that of the transpiration demand, which is a function of the total leaf area (relative to the soil volume exploited by the roots), the vapor pressure deficit, and the stomatal conductance. An inability to maintain this supply will result in a loss of leaf turgor and stomatal closure, and in extreme cases possibly damage the capacity to assimilate CO_2. The closure of the stomata will lead to a decrease in p_i as assimilation continues at a lower rate of CO_2 supply. The isotopic signal recorded in sugars during this period will be the production-weighted value, and will depend on the partial pressure of CO_2 (which will generate an isotopic signature in the produced sugars), and the assimilation rate (which will determine the amount of sugar generated with the specific isotopic signature), which decreases with decreasing p_i.

Investigating the changes in the ratio of leaf conductance to photosynthetic capacity, and ascribing ecological significance to those patterns, is complicated by the fact that the two parameters interact (Wong, Cowan & Farquhar 1979). In a series of experiments manipulating the growth conditions of several species, as well as the environmental conditions during the measurement of gas exchange, leaf conductances were found to correlate with photosynthetic capacity such that p_i remained remarkably constant (Wong, Cowan & Farquhar 1985a; Wong, Cowan & Farquhar 1985b; Wong, Cowan & Farquhar 1985c). The magnitude of both g and A may exhibit strong responses across a gradient of decreasing rainfall, which would have significant impacts on the performance of a species, but if g depends upon A, the resulting Δ signal may be quite small.

1.3 Influences on photosynthetic capacity

The diffusion of CO_2 through the stomata and into the sites of carboxylation, and the dependance of the rate of fixation on amount of Rubicso and regeneration of RuBP are relatively well understood (Farquhar, von Caemmerer & Berry 1980; von Caemmerer & Farquhar 1981). Rubisco accounts for the largest proportion of leaf nitrogen, and leaf photosynthetic capacities have been linked to leaf nitrogen concentrations at many scales (Field & Mooney 1986; Evans 1989; Evans 1989; Evans

1989; Schulze et al. 1994; Leuning et al. 1995). Reich et al. (1998) recently increased the predictive ability of the leaf nitrogen concentration: photosynthetic capacity relationship by including specific leaf area as a modifying parameter.

The main environmental influence translating potential photosynthetic capacity, as determined by leaf nitrogen investment, into actual photosynthetic demand is incident solar radiation. The position of the leaves in the canopy of the individual and its neighbors has the greatest influence on ambient light levels. Sampling Δ by leaves from the tops of emergent trees reduces the influences of shading on those leaf samples, but the wood samples of the same tree would be influenced by the total canopy architecture of the tree in relation to nearby trees.

Gradients in light levels through a canopy are stable stresses, and plants have been shown to adjust the allocation of nitrogen along the light gradient to maximize total canopy performance (Field 1983; Evans 1989). Of interest to a measure of the total canopy Δ signal, recorded in the wood tissue at the trunk, is the extent to which the profiles in leaf conductance match the profiles of photosynthetic demand determined by the canopy profiles of leaf nitrogen contents and light levels.

Although short-term water stress, such as that which occurs on a diurnal time-scale in afternoons with high vapor pressure deficits, primarily affects assimilation by reductions in stomatal conductance, longer-term water stress, such as that which occurs with the onset of a summer drought, may also result in lower maximum assimilation capacities (Escalona, Flexas & Medrano 1999). In an experiment where gas exchange parameters were measured on potted plants allowed to slowly dry, (Lajtha & Barnes 1991) found that instantaneous WUE of *Juniperus monosperma*, a drought-tolerant species, increased with soil drying from pre-dawn xylem pressure potentials of 0 to -3.5MPa, but then sharply decreased at lower values. This pattern could reflect decreasing stomatal conductances with a stable assimilation capacity, until water stress begins to directly impair the assimilation capacity. A second species they studied showed little change in assimilation or instantaneous WUE until the pre-dawn xylem pressure potentials reached -2.0MPa, when there was complete stomatal closure. Where there is a predictable annual drought cycle, as in the Northern Territory, and most species show some degree of canopy leaf area reduction, the annual pattern of leaf phenology and re-translocation of leaf nitrogen before leaf abscission may be hard to distinguish from a down regulation of photosynthetic capacity due to water-stress.

1.4 Influences on conductance

At any particular conductance, an increase in assimilation will decrease p_i. This could occur as a short-term response to an increase in light levels (Ehleringer et al. 1986; Flanagan, Cook & Ehleringer 1997), or as a long-term response to increased leaf nitrogen concentrations. Rubisco contents per unit leaf area determine assimilation rates, and reflect the growth strategies for the acquisition and allocation of nitrogen. Increasing the ability to remove CO_2 from the intercellular air spaces is a rather long-term strategy, when compared to the dynamics of stomata. It is also expensive in terms of nitrogen investment, since for each increment of investment the return decreases. It is reasonable to conclude that much of the signal recorded in the Δ values of plant tissues is a result of short-term variations in stomatal conductance. Carbon isotope discrimination provides an integrated measure of the stomatal limitation on photosynthesis.

Stomatal conductance is influenced by many external environmental conditions and internal physiological conditions, and there have been numerous models put forward attempting to integrate the observations. Jarvis & Davies (1998) emphasized the homoeostatic nature of internal CO_2 concentrations (Wong et al. 1979; Mott 1988) and developed a control equation for stomatal conductance based on the degree to which photosynthetic capacity is realized, as modified by the sensitivity to transpiration. The widely used empirical relation of Ball, Woodrow & Berry (1987), and the modified versions of Leuning (1990, 1995) and others (Collatz et al. 1991; Lloyd 1991; Aphalo & Jarvis 1993) integrates the observed interactions of evaporative demand, assimilation and CO_2 supply in determining stomatal conductance. In these models conductance is positively related to assimilation (or a function of temperature (Lloyd 1991), or both

(Aphalo & Jarvis 1993)), inversely related to CO_2 concentrations at the leaf surface, and constrained by either the relative humidity (Ball et al. 1987) or an inverse relationship to the vapor pressure deficit. Although these descriptions of the observations of stomatal response to selected environmental variables are useful when combined with models of photosynthesis (Baldocchi 1994), they do not provide insight into "what a plant should be doing" in terms of an optimal response to the conditions, or "how" a plant would achieve this response based on the underlying mechanisms of stomatal responses which might be applicable to explaining patterns of carbon isotope discrimination.

In order to maximize carbon gain and minimize water loss during a time period Cowan & Farquhar (1977) state that the sensitivity of transpiration to changes in conductance and the sensitivity of assimilation to these same changes in conductance should remain constant, yielding

$$\frac{\frac{\partial E}{\partial g}}{\frac{\partial A}{\partial g}} = \lambda . \qquad \text{Eq. 1.4}$$

Substituting expressions for E and A as functions of g (here taken to be the conductance to CO_2, $g_c = g/1.6$);

$$E = 1.6 g_c D \qquad \text{Eq. 1.5}$$

$$A = g_c (c_a - c_i) \qquad \text{Eq. 1.6}$$

(where D is the vapor pressure deficit and c_a and c_i are the ambient and internal CO_2 concentrations) and assuming carboxylation efficiency (k) is linear over the range of c_i occurring due to changes in stomatal conductance

$$A = k(c_i - \Gamma) \qquad \text{Eq. 1.7}$$

(where Γ is the CO_2 compensation point during assimilation) and taking their derivatives yields an expression for g that satisfies Equation 1.4, i.e.

$$g_c = k\left(\sqrt{\frac{\lambda(c_a - \Gamma)}{1.6D}} - 1\right) \qquad \text{Eq. 1.8}$$

(Cowan 1977). The linear approximation of the photosynthetic demand function can be eliminated, and an expression for stomatal control that provides optimal responses to the environmental conditions expressed as

$$g_c = \frac{A}{\sqrt{\frac{1.6}{\lambda} D(c_a - \Gamma)}} \qquad \text{Eq. 1.9}$$

(Farquhar et al. unpublished). This control function has not been used in many combined models of conductance and photosynthesis (see de Pury (1995)), possibly due to the introduction of λ which remained undetermined.

Although useful in describing "what a plant should do", Equation 1.9 does not address "how" a plant does it. As reviewed by Cowan (1977) and re-explored by Dewar (1995) stomatal aperture is related to guard cell turgor pressure, or more specifically, the difference in turgor pressure between the guard cells and subsidiary cells. Following the presentation of (Dewar 1995), the following;

$$E_s = k(\Psi_s - \Psi_l) \qquad \text{Eq. 1.10}$$

$$\Psi_l = P_l + \pi_l \qquad \text{Eq. 1.11}$$

$$g = \chi P_l \qquad \text{Eq. 1.12}$$

$$-E_t = gD \qquad \text{Eq. 1.13}$$

$$E_t = -E_s \qquad \text{Eq. 1.14}$$

can be combined to

$$g = \frac{k\chi(\Psi_s - \pi_l)}{k + \chi D} \qquad \text{Eq. 1.15}$$

where E_s is the flux of water from the soil to the leaves along the gradient in water potentials between the two (Ψ_s - Ψ_l) modified by the hydraulic conductivity *k*, the leaf water potential is the sum of the positive turgor pressure (P_l) and the (negative) osmotic potential π_l, conductance (*g*) is a function (χ) of turgor pressure, and transpiration ($-E_t$ away from the leaf) depends on the vapor pressure deficit (*D*). Conductance and leaf turgor reflect the balance between the rates of water supply (and the importance of hydraulic conductivity), and demand. The mechanisms included in Equation 1.15 do not open the stomata allowing photosynthesis, and only close them in response to soil water status or high evaporative demand. Allowing the osmotic potential to vary with assimilation (*A*), with a function such as

$$\pi_1 = \pi_0 - \frac{\pi_{\max} A}{k_\pi + A} \qquad \text{Eq. 1.16}$$

generates a drop in π_l between a minimal value (π_0) and a maximal value (π_{max}) with a sensitivity to *A* of k_π.

The longer-term dynamics of stomatal control, and the "carrying-forward" of information between days has been explored by including an ABA signal generated by root water potentials (Johnson et al. 1991; Tardieu 1993; Tardieu & Davies 1993). This signal could be used to simulate the lack of late afternoon recovery in stomatal conductance when VPD values decreased and plant water potentials increased as is often observed. The ABA signal could also be used to simulate the decrease of the maximum morning conductances as the soil dried over a series of days.

Although much of the study of the control of stomatal functioning has related to the responses to the environmental demands for water from the leaf, species which have been existing for many generations in a stable climate should have developed solutions to supply water at rates equal to that demand. The role of hydraulic conductivities, and "supply-side" constraints on leaf water status is becoming clearer (Yoder et al. 1994; Ryan & Yoder 1997; Hubbard, Bond & Ryan 1999).

The importance of low hydraulic conductivities in causing increasing stomatal sensitivity to evaporative demand may be greater in gymnosperms than angiosperms, as the tracheids of the former are usually thought to have higher resistance to water flow than the vessels of the latter. However, these differences may be primarily in the hydraulic conductivities of branches, and variations in other aspects of the hydraulic architecture may compensate, as no clear differences were found between whole-plant conductivities of several tropical angiosperms and conifers (Becker, Tyree & Tsuda 1999). In a study of 12 species of tropical trees sampled as saplings about 40% of the whole plant resistance to water flow was found to be in the leaves (Becker et al. 1999). About 25% of the resistance was attributable to the roots, and the remainder would be due to trunks and branches.

In reviewing the regulation of stomatal conductance of forest canopies Whitehead (1998) noted that the results of Read & Farquhar (1991) (that Δ was negatively correlated to rainfall at the site of origin for 22 *Nothofagus* species) were interpreted to suggest that species growing in drier climates would have evolved higher hydraulic conductivities so that conductance could continue during periods of high evaporative demand, and that when moved to a less stressful common garden, the arid species exhibited lower water-use efficiency than the mesic species. Also mentioned were the results of Williams & Ehleringer (1996) where one (*Quercus gambelii*) of three species showed negative correlations between Δ and measures of both water supply (annual rainfall and summer rainfall) and demand (growing season VPD and ω), while the other two species showed little correlation between Δ and the climatic parameters. *Quercus gambelii* seemed to not have the morphological plasticity of the other two species, allowing adjustments in hydraulic conductivity to maintain water supplies in the more stressful environments.

In terms of the understanding of patterns of Δ, these models of stomatal control either attempt to define a maximum conductance as a function of the environmental conditions, or as a function of the photosynthetic demand, which is a function of the environmental conditions. If conductance is tightly coupled to photosynthetic demand, then there will be little resultant Δ signal regardless of the dynamics of the environmental stresses.

1.5 The optimal balance between photosynthesis and conductance with increasing aridity

The optimal balance between the water and the nitrogen economies depends upon the relationship between assimilation and transpiration with increasing conductance. The common pathway of CO_2 uptake and water loss through stomata means any stomatal regulation of one activity will affect the other. Photosynthetic rate saturates as conductance increases, so the increase in A per unit increasing g is always decreasing.

Transpiration is a nearly linear function of conductance, as the external vapor pressure is constant and the internal vapor pressure is saturating at the leaf temperature (which is constant or may go down if the leaves are cooled by high rates of water loss). Instantaneous water-use efficiency (the ratio of carbon gain to water loss at the leaf level) therefore continuously decreases with increasing conductance.

Increases in water-use efficiency will therefore generally come about by decreasing conductance. With a fixed amount of available soil water the slower it is used the greater the final total carbon gain. With periodic additions to the soil water supply the optimal pattern of water use would be to use the water slowly, but ensure all of the water was used by the point of next addition. With a relatively stable interval between rainfall events, those individuals which use up all of their available water during the average drought length will accumulate the most carbon (Mäkela, Berninger & Hari 1996).

In a competitive environment it may be better to sacrifice high water-use efficiency for higher ability to capture some other resource. In the presence of competition it may be better to use all of the water well before the next rain and then sit with closed stomata, if this less efficient pattern of carbon gain allowed faster growth and therefore direct hindering of a competitor by usurping other resources (such as fast height growth which then shades a competitor). A necessary corollary of this strategy is the development of effective methods of stress tolerance, which is usually found to be at odds with fast growth (Chapin, Autumn & Pugnaire 1993). A freely draining soil with surface evaporation also complicates the pattern of water use, as faster rates of plant water use limit losses to runoff and surface evaporation. These concurrent abiotic processes may explain why juveniles with a small, shallow root systems are often less water-use efficient than adults.

For a given amount of water, defined by a storage capacity, a pattern of replenishment, and the competing biotic and abiotic uses of the water, there is an optimal pattern of water use. This water use depends upon the VPD (beyond the plant's control), the total canopy leaf area, and the conductance per unit leaf area. Given that lower conductance is more efficient, the plant should opt for high leaf area, with low conductance per unit area, to the limit of carbon availability to construct and maintain the leaf area. A minimum conductance may also be required by the need to cool the leaves in order to avoid permanent thermal damage. The return per unit leaf area then depends on the nitrogen investment in those leaves. Where conductance is constrained by the availability of water, the carbon return can be increased by increased nitrogen investment in the leaves. As substitutable resources for carbon gain, water-use efficiency and nitrogen-use efficiency are mutually exclusive (Field, Merino & Mooney 1983; Bloom, Chapin & Mooney 1985; Field & Mooney 1986; Chapin et al. 1987). The pattern of either maintaining high rates of conductance, and maintaining high p_i for high returns per unit N invested at the cost of high rates of water loss, or maintaining lower rates of conductance with lower p_i and low returns per unit N invested but with low rates of water loss are the extremes of the physiological strategies available to plants in arid environments. At different stages within a species alternative solutions may be best, as has been shown in juvenile and adult *Chrysothamnus nauseosus* where there is a decrease in NUE and an increase in WUE with age, with juvenile plants having lower nitrogen concentrations and keeping the stomata relatively more open (per unit A) than adults (Donovan & Ehleringer 1992).

In wet years wheat growth responded to the addition of fertilizer without a change in Δ, possibly reflecting the ability of g to increase with higher A, while in dry years growth showed little response to fertilizer, but Δ decreased, possibly reflecting an increased A being constrained by g and the resulting lower p_i not contributing large amounts of carbon gain (Jenkinson, Coleman & Harkness 1995).

Based on an understanding of the theoretical patterns of water-use efficiency there should be an overall decrease in conductance per unit leaf area with increasing aridity. Assimilation capacity should remain unchanged (per unit area), or increase as higher leaf nitrogen contents attempt to maximize the removal of CO_2 from the intercellular air spaces when photosynthesis becomes conductance limited. This reduction in conductance with a constant or increasing assimilation will result in a decreasing Δ with increasing aridity. This physiological stress precedes any morphological response the plant could make to minimize the stress. With increasing aridity these morphological responses will be limited to small modifications within the genetically defined over-all growth form. When these possibilities are exhausted, the inability to maintain transpiration will close the stomata and no longer allow a positive carbon balance.

The competing issues influencing carbon allocation have been reviewed by Cannell & Dewar (1994). The balance between the allocation of carbon to foliage and roots is influenced by the uptake and use of nutrients and water, and the allocation to trunks is influenced by the need to maintain a functioning transport system and the mechanical requirements of supporting the foliage mass. The demands of reproduction are distinctly different from the allocation patterns involved in vegetative structures due to the active transport of materials against concentration gradients into reproductive structures.

Mathematical expressions describing optimal stomatal behavior, with the goal of maximizing carbon gain per unit water loss, are relatively easy to develop because both carbon gain and water loss can be described as simple functions of conductance (Hari et al. 1986; Mäkela et al. 1996). Expanding the scope of the problem to include the trade off between conductance per unit leaf area and amount of leaf area, as well as the balance between leaf area (gaining carbon and using water) and the root length (using carbon and supplying the water) has been addressed by Givnish (1986). The solution to the optimization of the ratio of allocation to leaves versus roots equaled the ratio of stomatal conductance (g_s) to mesophyll conductance (g_m), which can be shown to be proportional to Δ. Adding Equation 2 to the derivation in Givnish (1986) yields

$$\frac{f}{1-f}=\frac{g_s}{g_m}=\frac{a+\frac{\Gamma}{c_a}(b-a)-\Delta}{\Delta-b}=\frac{\Delta-a-\frac{\Gamma}{c_a}(b-a)}{b-\Delta} \qquad \text{Eq. 1.17}$$

where f is the fractional allocation to leaves and 1-f is the fractional allocation to roots. From Equation 1.17 it would seem than there will be a unique relationship between stomatal and mesophyll conductance and the allocation of resources to leaves and roots, as well as to a specific Δ value. The relationship between Δ and g_s/g_m is non-linear and asymptotically approaches b.

Across a range of herbaceous species grown under non-limiting hydroponic conditions, there was a positive relationship between leaf Δ and the fraction of biomass allocated to the roots (root weight ratio) and the specific root length (root length divided by root weight) (Poorter & Farquhar 1994). The observed differences in Δ between these species correlated with transpiration and not with photosynthesis per unit leaf area, area-based leaf nitrogen concentration, or specific leaf area. Δ was also found to be positively correlated to root : shoot ratio among a variety of seedlings of white spruce

(Picea glauca) accessions grown at various levels of nitrogen and water supply (Livingston et al. 1999).

With decreasing water supply, whole plant morphology may adjust, and allocation to roots will increase at the expense of leaf area and height growth. Specific leaf area may decrease as there is not the water to support a large leaf area and denser leaves may be adaptive for stress tolerance. Plants from arid regions are selected for an ability to find and conduct water to the leaves. Therefore when moved to a wet common garden the over-supply of water keeps the stomata more open than mesic plants. Plants from more mesic areas seem to have greater stomatal sensitivity to evaporative demand, possibly due to lower hydraulic conductivities, and show lower conductances than arid plants in common environments with high VPD.

In highly variable, stressed environments, genetically fixed conservative behavior will be the only strategy which will guarantee persistence. Plastic modifications toward conservative behavior will always be reactive solutions, and although allowing greater performance in good times, be wasteful with the sudden onset of bad times. In more favorable environments, genetically fixed conservative behavior will not allow growth rates fast enough to compete with species without such constraints.

1.6 Literature Cited

Andersen, A.N., Braithwaite, R.W., Cook, G.D., Corbett, L.K., Williams, R.J., Douglas, M.M., Gill, A.M., Setterfield, S.A. & Muller, W.J. (1998) Fire research for conservation management in tropical savannas: Introducing the Kapalga fire experiment. Australian Journal of Ecology 23, 95-110.

Aphalo, P.J. & Jarvis, P.G. (1993) An analysis of Ball's empirical model of stomatal conductance. Annals of Botany 72, 321-327.

Baldocchi, D. (1994) An analytical solution for coupled leaf photosynthesis and stomatal conductance models. Tree Physiology 14, 1069-1079.

Ball, J.T., Woodrow, I.E. & Berry, J.A. (1987) A model predicting stomatal conductance and its contribution to the control of photosynthesis under different environmental conditions. In: Progress in Photosynthesis Research (J. Biggen), 221-224. Martinus Nijhoff Publishers, The Netherlands.

Becker, P., Tyree, M.T. & Tsuda, M. (1999) Hydraulic conductances of angiosperms versus conifers: similar transport sufficiency at the whole-plant level. Tree Physiology 19, 445-452.

Bloom, A.J., Chapin, F.S., III & Mooney, H.A. (1985) Resource limitation in plants - an economic analogy. Ann Rev Ecol Syst 16, 363-392.

Brooker, M.I.H. & Kleinig, D.A. (1994) Field Guide to Eucalypts: Volume 3 Northern Australia. Inkata Press, Sydney.

Cannell, M.G.R. & Dewar, R.C. (1994) Carbon allocation in trees: a review of concepts for modelling. Advances in ecological research 25, 59-104.

Chapin, F.S., III, Autumn, K. & Pugnaire, F. (1993) Evolution of suits of traits in response to environmental stress. Am. Nat. 142, S78-S92.

Chapin, F.S., III, Bloom, A.J., Field, C.B. & Waring, R.H. (1987) Plant responses to multiple environmental factors. BioScience 37, 49-57.

Chippendale, G.M. & Wolf, L. (1981) The Natural Distribution of *Eucalyptus* in Australia. Australian National Parks and Wildlife Servie, Canberra.

Collatz, G.J., Ball, J.T., Grivet, C. & Berry, J.A. (1991) Physiological and environmental regulation of stomatal conductance, photosynthesis and transpiration: a model that includes a laminar boundary layer. Agric. For. Meteorol. 54, 107-136.

Condon, A.G., Richards, R.A. & Farquhar, G.D. (1992) The effect of variation in soil water availability, vapour pressure deficit and nitrogen nutrition on carbon isotope discrimination in wheat. Aust. J. Agric. Res. 43, 935-947.

Cowan, I.R. (1977) Stomatal behaviour and environment. Adv Bot Res 4, 117-228.

Cowan, I.R. & Farquhar, G.D. (1977) Stomatal function in relation to leaf metabolism and environment. In: Integration of Activity in the Higher Plant, Society for Experimental Biology Symposium XXXI (D. H. Jennings), 471-505. Cambridge University Press, Cambridge.

de Pury, D.G.G. (1995) Scaling photosynthesis and water use from leaves to paddocks

Dewar, R.C. (1995) Intrepretation of an empirical model for stomatal conductance in terms of guard cell function. Plant, Cell and Environment 18, 365-372.

Donovan, L.A. & Ehleringer, J.R. (1992) Contrasting water-use patterns among size and life-history classes of a semi-arid shrub. Functional Ecology 6, 482-488.

Ehleringer, J.R. & Cooper, T.A. (1988) Correlations between carbon isotope ratio and microhabitat in desert plants. Oecologia 76, 562-566.

Ehleringer, J.R., Field, C.B., Lin, Z. & Kuo, C. (1986) Leaf carbon isotopes and mineral composition in subtropical plants along an irradiance cline. Oecologia 70, 520-526.

Escalona, J.M., Flexas, J. & Medrano, H. (1999) Stomatal and non-stomatallimitations of photosynthesis under water stress in field-grown grapevines. Australian Journal of Plant Physiology 26, 421-433.

Evans, J.R. (1989) Partitioning of nitrogen between and within leaves grown under different irradiances. Aust. J. Plant Physiol. 16, 533-548.

Evans, J.R. (1989) Photosynthesis - the dependence on nitrogen partitioning. In: Causes and consequences of variation in growth rate and productivity of higher plants (H. Lambers, M. L. Cambridge, H. Konings and T. L. Pons), 159-174. SPB Academic Publishing, The Hague.

Evans, J.R. (1989) Photosynthesis and nitrogen relationships in leaves of C_3 plants. Oecologia 78, 9-19.

Farquhar, G.D., Buckley, T.N., Miller, J.M., Santrucek, J. & Mott, K.A. (unpublished) Optimisation of stomatal behaviour. -.

Farquhar, G.D., O'Leary, M.H. & Berry, J.A. (1982) On the relationship between carbon isotope discrimination and the intercellular carbon dioxide concentration in leaves. Australian Journal of Plant Physiology 9, 121-137.

Farquhar, G.D. & Richards, R.A. (1984) Isotopic composition of plant carbon correlates with water-use efficiency of wheat genotypes. Australian Journal of Plant Physiology 11, 539-552.

Farquhar, G.D., von Caemmerer, S. & Berry, J.A. (1980) A biochemical model of photosynthetic CO_2 assimilation in leaves of C_3 species. Planta 149, 78-90.

Field, C. (1983) Allocating leaf nitrogen for the maximization of carbon gain: leaf age as a control on the allocation program. Oecologia 56, 341-347.

Field, C., Merino, J. & Mooney, H.A. (1983) Compromises between water-use efficiency and nitorgen-use efficiency in five species of California evergreens. Oceologia 60, 384-389.

Field, C. & Mooney, H.A. (1986) The photosynthesis - nitrogen relationship in wild plants. In: On the economy of plant form and function (T. J. Givnish), 25-55. Cambridge University Press, Cambridge.

Flanagan, L.B., Cook, C.S. & Ehleringer, J.R. (1997) Unusually low carbon isotope ratios in plants from hanging gardens in southern Utah. Oecologia 111, 481-489.

Givnish, T.J. (1986) Optimal stomatal conductance, allocation of energy between leaves and roots, and the marginal cost of transpiration. In: On the economy of plant form and function (T. J. Givnish), 171-213. Cambridge Univ Press, Cambridge.

Hari, P., Mäkelä, A., Korpilahti, E. & Holmberg, M. (1986) Optimal control of gas exchange. Tree Physiology 2, 169-175.

Hubbard, R.M., Bond, B.J. & Ryan, M.G. (1999) Evidence that hydraulic conductance limits photosynthesis in old *Pinus ponderosa* trees. Tree Physiology 19, 165-172.

Jarvis, A.J. & Davies, W.J. (1998) The coupled response of stomatal conductance to photosynthesis and transpiration. Journal of Experimental Botany 49, 399-406.

Jenkinson, D.S., Coleman, K. & Harkness, D.D. (1995) The influence of fertilizer nitrogen and season on the carbon-13 abundance of wheat straw. Plant and Soil 171, 365- 367.

Johnson, I.R., Melkonian, J.J., Thornley, J.H.M. & Riha, S.J. (1991) A model of water flow through plants incorporating shoot/root 'mesage' control of stomatal conductance. Plant, Cell and Environment 14, 531-544.

Lajtha, K. & Barnes, F.J. (1991) Carbon gain and water use in pinyon pine-juniper woodlands of northern New Mexico: field versus phytotron chamber measurements. Tree Physiology 9, 59-67.

Leuning, R. (1990) Modelling stomatal behaviour and photosynthesis of *Eucalyptus grandis*. Aust J Plant Physiol 17, 159-175.

Leuning, R. (1995) A critical appraisal of a combined stomatal-photosynthesis model for C_3 plants. Plant, Cell and Environment 18, 339-355.

Leuning, R., Kelliher, F.M., De Pury, D.G.G. & Schulze, E.-D. (1995) Leaf nitrogen, photosynthesis, conductance and transpiration: scaling from leaves to canopies. Plant, Cell and Environment 18, 1183-1200.

Livingston, N.J., Guy, R.D., Sun, Z.J. & Ethier, G.J. (1999) The effects of nitrogen stress on the stable isotope composition, productivity and water use efficiency of white spruce (*Picea glauca* (Moench) Voss) seedlings. Plant, Cell and Environment 22, 281-289.

Lloyd, J. (1991) Modelling stomatal responses to environment in *Macadamia integrifolia*. Aust. J. Plant Physiol. 18, 649-660.

Mäkela, A., Berninger, F. & Hari, P. (1996) Optimal control of gas exchange during drought: Theoretical analysis. Annals of Botany 77, 461-467.

Mott, K.A. (1988) Do stomata respond to CO_2 concentrations other than intercellular? Plant Physiol 86, 200-203.

Pole, M.S. & Bowman, D.M.J.S. (1996) Tertiary plant fossils from Australia's 'Top End'. Australian Systematic Botany 9, 113-126.

Poorter, H. & Farquhar, G.D. (1994) Transpiration, intercellular carbon dioxide concentration and carbon-isotope discrimination of 24 wild species differing in relative growth rate. Aust. J. Plant Physiol. 21, 507-516.

Read, J. & Farquhar, G. (1991) Comparative studies in *Nothofagus* (Fagaceae). I. Leaf carbon isotope discrimination. Functional Ecology 5, 684-695.

Reich, P.B., Ellsworth, D.S. & Walters, M.B. (1998) Leaf structure (specific leaf area) modulates photosynthesis-nitrogen relations: evidence from within and across species and functional groups. Functional Ecology 12, 948-958.

Ryan, M.G. & Yoder, B.J. (1997) Hydraulic limits to tree height and tree growth. BioScience 47, 235-242.

Schulze, E.-D., Kelliher, F.M., Körner, C., Lloyd, J. & Leuning, R. (1994) Relationships among maximum stomatal conductance, ecosystem surface conductance, carbon assimilation rate, and plant nitrogen nutrition: A global ecology scaling exercise. Annu. Rev. Ecol. Syst. 25, 629-660.

Skarpe, C. (1992) Dynamics of savanna ecosystems. Journal of Vegetation Science 3, 293-300.

Tardieu, F. (1993) Will increases in our understanding of soil-root relations and root signalling substantially alter water flux models? Phil. Trans. R. Soc. Lond. B 341, 57-66.

Tardieu, F. & Davies, W.J. (1993) Integration of hydraulic and chemical signalling in the control of stomatal conductance and water status of droughted plants. Plant, Cell and Environment 16, 341-349.

von Caemmerer, S. & Farquhar, G.D. (1981) Some relationships between the biochemistry of photosynthesis and the gas exchange of leaves. Planta 153, 376-387.

Walcroft, A.S., Silvester, W.B., Whitehead, D. & Kelliher, F.M. (1997) Seasonal changes in stable carbon isotope ratios within annual rings of *Pinus radiata* reflect environmental regulation of growth processes. Australian Journal of Plant Physiology 24, 57-68.

Walter, H. (1973) Vegetation of the Earth. Springer-Verlag, Berlin.

Whitehead, D. (1998) Regulation of stomatal conductance and transpiration in forest canopies. Tree Physiology 18, 633-644.

Williams, D.G. & Ehleringer, J.R. (1996) Carbon isotope discrimination in three semi-arid woodland species along a monsoon gradient. Oecologia 106, 455-460.

Williams, R.J., Cook, G.D., Gill, A.M. & Moore, P.H.R. (1999) Fire regime, fire intensity and tree survival in a tropical savanna in northern Australia. Australian Journal of Ecology 24, 50-59.

Williams, R.J., Duff, G.A., Bowman, D.M.J. & Cook, G.D. (1996) Variation in the composition and structure of tropical savannas as a function of rainfall and soil texture along a large-scale climatic gradient in the Northern Territory, Australia. Journal of Biogeography 23, 747-756.

Williams, R.J., Myers, B.A., Muller, W.J., Duff, G.A. & Eamus, D. (1997) Leaf phenology of woody species in a north Australian topical savanna. Ecology 78, 2542-2558.

Wilson, B.A., Brocklehurst, P.S., Clark, M.J. & Dickinson, K.J.M. (1990) Vegetation survey of the Northern Territory, Australia. Technical Report No. 49. Conservation Commission of the Northern Territory, Australia, Darwin.

Wong, S.C., Cowan, I.R. & Farquhar, G.D. (1979) Stomatal conductance correlates with photosynthetic capacity. Nature 282, 424-426.

Wong, S.-C., Cowan, I.R. & Farquhar, G.D. (1985a) Leaf conductance in relation to rate of CO_2 assimilation I. influence of nitrogen nutrition, phosphorus nutrition, photon flux density, and ambient partital pressure of CO_2 during ontogeny. Plant Physiol. 78, 821-825.

Wong, S.-C., Cowan, I.R. & Farquhar, G.D. (1985b) Leaf conductance in relation to rate of CO_2 assimilation II. effects of short-term exposures to different photon flux densities. Plant Physiol. 78, 826-829.

Wong, S.-C., Cowan, I.R. & Farquhar, G.D. (1985c) Leaf conductance in relation to rate of CO_2 Assimilation III. influences of water stress and photoinhibition. Plant Physiol. 78, 830-834.

Yoder, B.J., Ryan, M.G., Waring, R.H., Schoettle, A.W. & Kaufmann, M.R. (1994) Evidence of reduced photosynthetic rates in old trees. Forest Science 40, 513-527.

Chapter 2

Research goals and thesis structure

2.1 Research goals

The goal of this work was to increase the understanding of the environmental controls on the distribution of selected *Eucalyptus* species along a rainfall gradient in the Northern Territory of Australia. The underlaying hypothesis was that these species represent growth strategies, primarily in carbon allocation patterns towards resource uptake, which are competitively successful in zones along the resource gradient. With decreasing rainfall species have to allocate more resources towards root growth, with less available for height growth and competition for light. Species distributions are therefore assumed to be bounded by an inability to acquire water at sufficient rates to maintain stomatal conductance on the xeric extreme, and an inability to compete for light on the mesic extreme. The pattern of increasing stomatal limitation on photosynthesis with decreasing rainfall across the distribution of the species will result in decreasing carbon reserves for defensive compounds such that the xeric distributional limit probably does not reflect the absolute physical limitations of the growth strategy, but one determined by the combination of water stress and other factors such as herbivory and pathogens.

The carbon isotope discrimination during the initial steps of photosynthesis, which reflects the ratio of stomatal conductance to assimilation capacity, leaves a signal in tissues subsequently created by the photosynthate. The expected response of Δ recorded in leaf and wood tissues across the distribution of each species across the environmental gradient should reflect increasing periods of water stress and stomatal closure. It was hypothesized that leaves may record a narrow time window when they are formed, and conditions during the wet season (when leaves are formed) may result in little stomatal closure. However, the stomata may not be able to remain open during the dry season and the wood samples collected at the base of the tree integrating photosynthate from the complete canopy throughout the full year may record a stronger response. Intra-annual reductions in the total canopy leaf area could allow the remaining leaves a greater water supply and reduce the water-stress signal in wood Δ. Low production when the stomata are fully closed would also not generate significant wood growth with a signal indicating stress. Even with the possibility of considerable morphological plasticity affecting such important parameters as root:shoot ratio the pattern of rainfall and species distributions should be reflected in mature plant physiological performance.

Given that the sampled species were closely related and of similar growth-form it was hypothesized that they would respond similarly to decreasing water availability. It was hypothesized that there would be similar, decreasing patterns in Δ with decreasing total annual rainfall across the distribution of each species reflecting the decreasing ability to maintain stomatal conductance relative to photosynthetic capacity. Where mesic species co-occur with replacement species with more xeric distributions, the xeric species should have higher Δ values reflecting the different morphological characters - specifically the increased absorbing root : leaf area ratio allowing better water supply per unit leaf area and therefore increased ability to maintain stomatal opening and a positive carbon balance.

The replacement of Eucalypts by *Acacia* species with decreasing rainfall, as is generally the pattern throughout Australia, would seem to indicate a trade off between high nitrogen-use efficiency in the mesic areas and high water-use efficiency in the xeric areas. Water and nitrogen are both required resources for successful carbon assimilation, and a lack of one can to some extent be offset by increased use of the other. It was hypothesized that resource substitution, specifically of nitrogen for water with decreasing water availability, was occurring within the series of sampled *Eucalyptus* species, as well as with the replacement of the genus. Resource substitution would explain the oft observed pattern of increasing leaf nitrogen concentrations with decreasing water availability.

The pattern of increasing leaf investment with decreasing water availability, both in terms of leaf nitrogen contents but also in terms of leaf carbon contents was hypothesized to increase the period of time required to pay back the carbon costs of leaf creation. It was hypothesized that gas exchange parameters that can be estimated from leaf nitrogen contents and leaf Δ could be used to calculate leaf payback periods which would increase across the distribution of each species with decreasing total annual rainfall. Increasing leaf payback periods would indicate the decreasing ability of the species to maintain a positive carbon balance, which should be critical in determining the distribution of the species.

Variation in Δ values can be generated by variation in either leaf conductances or assimilation capacity, but in naturally occurring, rain-fed plants, variation in leaf conductance should occur at a higher frequency than variations in assimilation capacity, resulting in patterns of Δ predominantly reflecting patterns of leaf conductance. It was hypothesized that Δ should be correlated with the calculated leaf conductances to a greater degree than to the calculated assimilation capacities. Carbon isotope discrimination should also show correlations with those environmental factors that influence leaf conductance independently from assimilation capacity, specifically parameters concerning water supply and evaporative demand.

Plants from low resource environments have been found to have inherently low growth rates, and low rates of resource uptake when moved to resource-rich environments. Physiological and morphological plasticity of a species growth strategy should allow a species to survive under a wide range of environmental conditions. However, under conditions of high environmental stress and significant variability a fixed, conservative resource-use growth strategy may preclude an individual from over-responding to temporary improvements in conditions that may not allow completion of reproduction. It was hypothesized that the ability to vary characteristics such as Δ would allow species to have wide distributions under conditions of high water availability, but with decreasing water availability species would show decreasing plasticity in these traits. Plasticity of physiological and morphological characters should be linked to both the location of a species along the gradient of decreasing resource, as well as to the size of the distribution of the species along the gradient.

And finally, it was proposed that measuring tissue Δ and nitrogen contents would be a fast and appropriate survey method that would allow the subsequent, focused measurement of gas exchange parameters being predicted.

2.2 Thesis structure

The following five Chapters describe five issues in ecophysiology and the environmental controls on the distributions of species. They are related primarily because they rely on subsets of the same basic data. Each Chapter is meant to be a complete, stand-alone description of the research addressing the specific issue and has therefore been written in the format of a complete scientific paper. There is some minor duplication of methods and discussion of necessary data resulting from this format.

The field sampling was conducted during September and October 1996, which is the end of the dry-season. Sampling was conducted in the Northern Territory along northern half of the Stuart Highway which runs in a north-south direction across the center of Australia. The most obvious feature of the environmental gradient is the decrease in mean annual rainfall from around 1600 mm in the north to around 200 mm in the south. The transect in this study is near the sites of the Northern Australian Tropical Transect (NATT), one of a series of the continental-scale transects of the IGBP core project Global Change and Terrestrial Ecosystems and those of the Cooperative Research Centre for the Sustainable Development of Tropical Savannas.

Dominant *Eucalyptus* overstory species were selected for study based on their distributions. It was hypothesized that these species would represent alternative growth strategies which would be successful in sub-regions along the environmental gradient. However, further research will be necessary to determine exactly why some of these species seem to replace one-another, while others co-exist.

Chapter 3, entitled 'Carbon isotope discrimination by a sequence of *Eucalyptus* species along a rainfall gradient in the Northern Territory, Australia' addresses this issue of the environmental controls on the distribution of species along an environmental gradient by using carbon isotope discrimination as a measure of plant strain in response to increasing environmental stress. The goal was to see if species distributions could be related to water availability, and if patterns of carbon isotope discrimination would reflect these environmental impacts.

Given that plants require multiple resources for growth, an obvious gradient in a single resource may not reflect an equivalent gradient in all other necessary resources. In some cases plants may be able to shift the ratio of resource-use when one resource becomes limiting. Chapter 4 on 'Resource substitution and leaf nitrogen concentrations in a sequence of *Eucalyptus* species along a rainfall gradient in the Northern Territory, Australia' explores the theory describing this phenomena and then analyzes the observed patterns along the transect based on the developed theoretical understanding.

'Scaling-up' leaf-level measurements of the fluxes of water, CO_2, energy, and other gases has become necessary in order to understand and predict the effects of increasing atmospheric greenhouse gases. By 'Using carbon isotope discrimination, leaf nitrogen concentration, and specific leaf area data to estimate continental-scale ecophysiologically important gas exchange parameters', Chapter 5 attempts to contribute to this scaling exercise.

Carbon isotope discrimination, as will be developed later, reflects the balance between the plant water-use and photosynthetic capacities at the leaf-level. Chapter 6 on the 'Environmental correlates of leaf and wood carbon isotope discrimination at the species and functional type levels in Australian *Eucalyptus* species' attempts to identify the important environmental influences on the observed patterns of carbon isotope discrimination in the naturally occurring overstory tree species.

The idea that species reflect a collection of genetically determined growth characteristics was explored in Chapter 7 on 'Plasticity of carbon isotope discrimination and other characteristics in *Eucalyptus* species along an environmental gradient in the Northern Territory, Australia'. The goal of the Chapter was to see if there were changes in the ability to vary plant characteristics with changes in resource availability, and if physiological or morphological characteristics were more commonly adjusted.

Chapter 3

Carbon isotope discrimination by a sequence of *Eucalyptus* species along a rainfall gradient in the Northern Territory, Australia[1]

---

[1] This chapter has been published as:

Miller JM, Williams RJ, Farquhar GD (2001) Carbon isotope discrimination by a sequence of *Eucalyptus* species along a subcontinental rainfall gradient in Australia. Functional Ecology 15(2): 222-232.

Summary

1. The carbon isotope discrimination (Δ) by a series of co-occurring and replacement *Eucalyptus* species was measured across an eight-fold decrease in rainfall. Since Δ is a measure of the stomatal limitation on photosynthesis it should provide a sub-continental scale measure of water-limited plant physiological performance.

2. With decreasing rainfall the whole-tissue leaf Δ of five of 13 species decreased, seven exhibited no trend, and one increased. The whole-tissue wood Δ of eight species decreased, showed no trend in four species, and increased in one species.

3. Species replacements were marked by a shift in Δ reflecting greater stomatal limitation on assimilation.

4. Wood Δ exhibited less variability than leaf Δ values.

5. There was a non-linear response of the multi-species average leaf and wood Δ to decreasing mean annual rainfall. This response reflected the spatial pattern of the sensitivities of Δ to decreasing rainfall of the individual species and was not the result of a proposed emergent behavior where the mean would differ from the responses of the individual species.

6. Patterns of Δ across the distributions of species (reflecting increasing stomatal limitation on assimilation) did not provide a simple measure of the physiological limits of the distribution of eucalypts in northwestern Australia.

3.1 Introduction

Northwestern Australia is characterized by a pronounced rainfall gradient from the mesic coastal and subcoastal landscapes to the semi-arid and arid interior. The dominant vegetation is tropical savanna trees, predominantly *Eucalyptus*, over a grassy understory (Williams et al. 1996). Many of the dominant *Eucalyptus* species in the savannas are distributed in bands perpendicular to the rainfall gradient (Brooker & Kleinig 1994), and there is a pronounced pattern of species replacements amongst the eucalypts across the rainfall gradient. The ability of the species to withstand decreasing water availability must play a role in determining the distributions of the species. By examining broad-scale patterns of carbon isotope discrimination (Δ) in the eucalypts, as a long-term integrative measure of stomatal limitation on photosynthesis, the link between the distributions of the species and the physiological performance of the adults was investigated.

The Δ recorded in plant tissues measures the internal partial pressure of CO_2 (p_i) during photosynthesis (A), reflecting the balance between rates of CO_2 supply to, and demand from, the intercellular air spaces (Farquhar et al. 1982). Carbon isotope discrimination is negatively related to A/g_c where g_c, the conductance of CO_2 into a leaf, depends upon the plant being able to sustain the co-occurring transpiration (E), which requires the acquisition and transport of water at rates equal to the evaporative demand. Due to the saturating response of A to increasing p_i, Δ provides a non-linear measure of plant performance. With a fixed photosynthetic capacity, changes in Δ due to changes in g_c at high Δ values reflect less of a change in A than similar changes at low Δ. Decreases in Δ can arise from either decreases in g_c or increases in photosynthetic capacity, and while both reflect increased stomatal limitation on A, the two sources of variation in Δ may result in opposite impacts on plant performance, especially when coupled with simultaneous changes in leaf area. A high Δ plant may be more productive (per unit leaf area) than a co-occurring low Δ plant when the low Δ signal is due to low g_c rather than high photosynthetic capacity. The amount of photosynthate produced at a given p_i will weight the subsequent Δ value of the tissues. Periods with sufficient water availability, and therefore high A and Δ, may dominate the signal recorded during periods of low water availability when there is both a low A and low Δ.

It seems reasonable that plants should respond to decreasing moisture availability (either in time or space) by decreasing stomatal conductance relative to photosynthetic capacity, generating patterns of decreasing Δ (Ehleringer & Cooper 1988; Comstock & Ehleringer 1992; Ehleringer 1994; Williams & Ehleringer 1996; Schulze et al. 1998). At some point this increasing stomatal limitation on carbon gain could place a species at a competitive disadvantage compared to other species that have morphological characteristics better suited to the acquisition of water under conditions of increasing aridity. These morphological features could include less allocation to the growth of leaf area and trunk height, and more to root length and depth. The difference in allocation patterns could segregate the alternative growth strategies along a moisture gradient, with the species with more root allocation experiencing less stomatal limitation on carbon gain in drier areas, but being unable to maintain its canopy position in wetter areas. Where the two species co-occur, there could be a clear difference in the Δ, with the species from the drier areas (the "xeric" species) having higher Δ values than the species from the wetter area (the "mesic" species).

This pattern of higher Δ in plants from dry environments has been found in several common garden experiments comparing a range of closely related species and ecotypes (Read & Farquhar 1991; Hubick & Gibson 1993; Zhang, Marshall & Jaquish 1993; Zhang & Marshall 1995; Lauteri et al. 1997). However, the opposite pattern, with species from arid areas maintaining lower Δ when grown in common gardens, reflecting a genetic selection for a high level of stomatal limitation on assimilation, has been found for ecotypes of a single species (Comstock & Ehleringer 1992) , for *Eucalyptus microtheca* in dry soil (Li et al. 2000), and for several other *Eucalyptus* species (Anderson et al. 1996).

If each species along a gradient of decreasing rainfall exhibits declining Δ values, and species with more xeric distributions exhibit less stomatal limitation on assimilation where species overlap, then there will be a repeating 'saw-toothed' pattern of decreasing Δ values (Figure 3.1). The pattern of the multi-species average Δ under conditions of decreasing rainfall will be fundamentally different from the responses of the individual species. The average Δ will show less sensitivity to environmental conditions, supporting the idea that biodiversity stabilizes land-surface gas exchange relationships.

In an earlier study in the Northern Territory along a rainfall gradient from 1800 to 200 mm yr^{-1} the average Δ of the leaves of the sampled overstory species exhibited little change until rainfall dropped below 475 mm yr^{-1}, where Δ then declined with decreasing rainfall (Schulze et al. 1998). This was fundamentally different from the pattern found along a rainfall gradient in south-eastern Queensland, Australia, where there was a linear decline (with a slope of 3.3‰ per meter of long-term mean annual rainfall) of a community-averaged leaf Δ with decreasing rainfalls between 1700 and 350 mm yr^{-1} (Stewart et al. 1995). It was proposed that the lack of response of the average Δ of overstory tree species to decreasing rainfall in the NT was due to the pattern of species replacements outlined above and to the failure of the trees to survive under the most arid conditions (Schulze et al. 1998).

As Δ in tissues records the $^{13}CO_2$ discrimination that occurred during the original assimilation events, leaf Δ and wood Δ may record different sub-annual periods. Leaf Δ values reflect conditions during a narrow time window when they are formed, assuming they are exclusively constructed of current photosynthate. Leaf longevity is one year or less and in some Northern Territory *Eucalyptus* species leaf flushing occurs just before the wet season when vapor pressure deficits drop and pre-dawn water potentials are high, resulting in conditions that may lead to little stomatal closure or patterns in leaf Δ (Myers et al. 1997; Williams et al. 1997; Myers et al. 1998). On the other hand wood, assumed to be produced throughout the year, may show a stronger response than the leaf tissues as it would include a production-weighted isotopic signal that includes the four month dry season when almost no rain occurs in Australian savannas.

The aim of this research was to see if the environmental limits on the distribution patterns of a sequence of dominant *Eucalyptus* species could be inferred from patterns of Δ. It was expected that a key element defining the pattern of species distributions would be the ability to maintain conductance relative to photosynthesis under periods of water stress. It was hypothesized that Δ would decrease with decreasing mean annual rainfall across the distribution of each species. Species from more arid areas were expected to exhibit higher Δ values where they overlapped with species from wetter areas. The differences in performance of the components of the community were expected to contribute to an emergent behavior fundamentally different from the behavior of the individual components. There should be a non-linear relationship between Δ and mean annual rainfall, with little change in Δ per unit decrease in rainfall at high rainfalls and larger changes in Δ with the same decrease in rainfall at lower rainfalls, because most of the patterns in Δ are assumed to be due to changes in g_c rather than photosynthetic capacity. These hypotheses where tested by measuring Δ in both leaf and wood samples from the dominant and sub-dominant Eucalypts across an eight-fold rainfall gradient. Leaf Δ was examined to see if the Δ recorded in leaves reflected an optimal, sub-annual period, while wood Δ was measured to see if there was a stronger stress signal that reflected growth over the full season.

3.2 Methods

Carbon isotope discrimination (Δ) was measured along the Northern Australian Tropical Transect (NATT), one of a series of the continental-scale transects of the IGBP core project Global Change and Terrestrial Ecosystems (Koch et al. 1995) that has been established to examine the responses of ecosystems to global environmental change. The transect runs from the Darwin region on the north coast of the Northern Territory (~ 12 ½°S) to the Tanamai Desert region at 18-19°S. Across the transect, and further south to the southern border of the Northern Territory (~ 25°S) there is an eight-fold decrease in mean annual rainfall from 1600 to 200 mm yr^{-1} (Figure 3.2a). Around 80% of the rain occurs during the four months from December to March (the wet-season) in the northern half of the transect. As latitude increases the rainfall becomes less seasonal and more variable, and at the southern edge of the transect only 50% of the rainfall occurs during the wet-season (Cook & Heergeden 1997; Heerdegen & Cook 1999). The annual average mid-afternoon saturation vapor pressure deficits (SVPD), calculated from the predicted wet and dry bulb temperatures, are shown in Figure 3.2b. During the wet season SVPD increased from 12°S latitude to around 20°S (where rainfall is about 400 mm yr^{-1}), but was relatively uniform further south into the drier areas. The sampling protocol attempted to evenly space the collections along the Stuart Highway (Figure 3.2c), which meant the collection intervals in terms of changes in rainfall between zones were greater in the north than in the south.

Dominant *Eucalyptus* species with mapped distributions (Brooker & Kleinig 1994) were selected *a priori* to include those restricted to the wetter northern end of the transect (*E. miniata* A.Cunn. Ex Schauer, *E. tetrodonta* F.Muell., and *E. tectifica* F.Muell.), the middle of the transect (*E. chlorophylla* Brooker & Done, *E. confertiflora* F.Muell., *E. pruinosa* Schauer, *E. coolabah* Blakely & Jacobs subsp. *coolabah*, *E. leucophloia* Brooker subsp. *QQ*, and *E. dichromophloia* F.Muell.), and the drier southern end of the transect (*E. terminalis* F.Muell., *E. odontocarpa* F.Muell., *E. pachyphylla* F.Muell., and *E. gamophylla* F.Muell.). Species with restricted distributions (possibly linked to specific soil types) were avoided, although *E. tectifica*, *E. chlorophylla* and *E. odontocarpa* have relatively narrow distributions. *E. pruinosa*, *E. leucophloia*, and *E. dichromophloia* have wide distributions, and *E. terminalis* was selected because it has an extremely wide distribution. Most of the species are evergreen, although *E. confertiflora* is completely dry-season deciduous. Adult *E. confertiflora* and *E. pruinosa* retain the juvenile leaf-form, while the other species switch to the adult leaf-form at maturity. *E. odontocarpa*, *E. pachyphylla*, and *E. gamophylla* are multi-stemmed mallee shrubs about 4 m tall, while the other species were single stemmed trees.

Sampling was conducted along 1750 km of the Stuart Highway between Darwin and the southern border of the Northern Territory. This distance was divided into 33 zones (each about 50 km long). The species that occurred in each zone were sampled once per zone at locations where they were locally abundant. Not all species within a zone occurred at the same location as a mixed stand, so samples were collected at 97 locations. Most of the locations were flat, and sampling was restricted to loams and sandy soils, as the species of interest were not common on clay soils (Williams et al. 1996). There was no stratification in sampling for soil type. Sampling was conducted at locations accessible from the highway at the end of the dry season between 16

September and 18 October 1996.

Sun-exposed leaves from the upper part of the canopy and wood samples were collected from five individuals of each species per zone for isotopic analysis. The material from each individual was analyzed separately to record the variability within the population. Ten leaves from one branch were bulked to comprise the leaf material for each individual tree. Wood material was collected as shavings from a hand drill from two holes per individual or as a basal disk for the smallest trees and the mallee growth-forms. The drill was able to penetrate approximately 100 mm after the bark had been removed. The exact number of years each wood sample represents could not be determined. In the wetter areas, where the annual growth increments are larger, there are probably fewer years represented than in the drier areas.

Leaf and wood material was air dried in the field and re-dried to a constant weight at 80°C back in the laboratory. Samples were finely ground in either a cyclone mill or, if the samples were very small, in a ball mill. Repeated measures of both the reference (ANU beet sugar) and selected *Eucalyptus* samples usually had standard deviations of around 0.1‰. Carbon isotope ratios were measured by an Isochrom on-line mass spectrometer after combustion in a Carlo Erba (Milano) elemental analyzer. Carbon isotope ratios were converted to carbon isotope discrimination (Δ in ‰) by assuming an isotopic composition value for air of -7.8‰ relative to PDB (Farquhar et al. 1982).

From the latitudes and longitudes recorded in the field with a GPS and the elevations predicted from a digital elevation map of Australia, relevant mean climatological parameters were predicted for the 97 locations where sampling occurred using ANUCLIM 1.8 (Centre for Resource and Environmental Studies, ANU), which is a software product that generates continuous splined surfaces of environmental parameters for the entire continent of Australia. Linear regressions of leaf and wood Δ on mean annual rainfall were calculated on the full data set and plotted together with the zone mean and standard errors (SAS 6.12, SAS Institute Inc.; Microcal Origin 5.0). The differences between species within a zone, and overall, were tested with a 1-way ANOVA followed by a Student-Newman-Kuels multiple range test (PROC GLM, SAS).

3.3 Results

The response of both leaf and wood Δ to declining rainfall for the 13 individual species varied (Figure 3.3). Leaf Δ decreased ($P < 0.05$) in five of the species (*E. miniata*, *E. pruinosa*, *E. leucophloia*, *E. dichromophloia*, and *E. terminalis*), showed no response in seven species (*E. tetrodonta*, *E. tectifica*, *E. confertiflora*, *E. coolabah*, *E. odontocarpa*, *E. pachyphylla*, and *E. gamophylla*), and increased in one species (*E. chlorophylla*). The wood Δ values decreased in eight of the species (*E. miniata*, *E. tetrodonta*, *E. pruinosa*, *E. leucophloia*, *E. coolabah*, *E. dichromophloia*, *E. terminalis*, and *E. odontocarpa*), showed no response in four of the species (*E. tectifica*, *E. chlorophylla*, *E. confertiflora*, and *E. gamophylla*), and increased in one species (*E. pachyphylla*).

The change in leaf Δ with decreasing rainfall across the distribution of individual species varied between +1‰ to -3‰, and the change in wood Δ varied between +0.5‰ to -2.5‰. The species with the greatest ability to withstand increases in the stomatal limitation on photosynthesis (i.e. had the most negative changes in Δ) had the widest distributional ranges. The two species that had positive changes in Δ with decreasing rainfall had narrow distributional ranges. The direction and the magnitude of the response of both leaf and wood Δ did not relate to the location of the species along the transect.

E. miniata and *E. tetrodonta* are the co-dominant trees defining many of the vegetation types north of ~15°S along this transect, and *E. miniata* showed patterns of Δ that indicated a greater sensitivity than *E. tetrodonta* to the decreasing rainfall from north to south. The only completely dry-season deciduous species sampled, *E. confertiflora*, showed no trend in Δ values with decreasing rainfall across its distribution. The ranges in the leaf Δ values of the tree species overlapped and there were no clear break points separating significantly different subgroups. The three mallee shrubs had leaf Δ values that were lower than all of the tree species. The rank order of the species wood Δ values was not the same as the leaf Δ, but the range in values found across the distributions of each species meant most of these differences were not significant.

The species mean leaf Δ values were between 0.9‰ and 1.9‰ higher than the wood Δ values, except for *E. pachyphylla* where the leaves averaged only 0.1‰ higher. In *E. pruinosa* and *E. pachyphylla* the difference between the leaf and wood Δ decreased with decreasing rainfall, and in *E. gamophylla* it increased, while the other species exhibited constant differences between leaf and wood values across their distributions.

With decreasing rainfall, the leaf Δ of new species (with a more xeric distribution than those already being sampled) was similar to the top ranked species found within the zone in one case, similar to the middle ranked species in five cases, and similar to the bottom ranked species in eight cases (Table 3.1). The wood Δ of the new species was similar to the top ranked species in three cases, the middle species in two cases, and the bottom species in five cases. At the xeric edge of the distributions of the species the leaf Δ of the departing species was similar to the highest ranked species in four cases, the middle ranked species in four cases and the lowest ranked species in four cases. The wood Δ of the departing species was similar to the top ranked species in five cases, the middle ranked species in three cases, and the lowest ranked species in four cases. Where species were sampled at exactly the same location (as opposed to within the 50 km zone) there were 28 possible pair-wise comparisons of mesic and xeric species. In seven cases the species with the distribution centered on lower rainfall areas (the xeric species) had significantly higher leaf Δ and in three cases significantly higher wood Δ. In four cases the mesic species had higher leaf Δ and in six cases higher wood Δ. In the remaining contrasts the values were not significantly different.

The proposed saw-toothed pattern of the individual species responses was not consistently evident (Figure 3.4). The non-linear response of the zone mean Δ values to decreasing mean annual rainfall reflected the spatial differences in the sensitivity of the response of Δ to decreasing rainfall of individual species (Figure 3.5). Species occurring at the wetter, northern end of the transect exhibited less change in both leaf and wood Δ values per unit decrease in rainfall than those occurring in the drier south. Although the slopes of the responses of both measures of Δ to decreasing rainfall became more negative with decreasing rainfall, two of the three highly positive values occurred in *E. pachyphylla* and *E. gamophylla* which were restricted to the driest areas of the transect.

Across the transect the responses of *Eucalyptus* leaf and wood Δ to decreasing mean annual rainfall were described by third-order polynomials. These explained 45% of the variability in the leaf Δ of the full data set (n = 645), and 59% of the variability in the wood Δ. Near the midpoint of the transect, where rainfall was around 700 mm yr^{-1} the species restricted to the wetter end of the transect were replaced by those with intermediate distributions, and there was a distinct step decrease in the mean wood Δ values. Where rainfall was less than 400 mm yr^{-1} there were usually only two species present, the isolated tall tree *E. terminalis* and either of the multi-stemmed mallee shrubs *E. pachyphylla* or *E. gamophylla*. The variability of the zone means reflects both the variability in Δ of *E. terminalis* and the differences between the two growth-forms.

3.4 Discussion

Patterns of Δ across the distribution of species

This study is the first to systematically sample Δ across the distributions of a series of replacement species along an environmental gradient. It views variation in Δ as resulting primarily from variation in CO_2 supply into, rather than demand from the intercellular air spaces within the leaves, and tests a synthetic framework that explains both species and growth-form level patterns. Unfortunately, using Δ as an index of stomatal limitation on assimilation is plagued by the ambiguity of the signal resulting from movements of both g_c and photosynthetic capacity. Increased whole-plant carbon gain could occur by increased g_c raising p_i and Δ with a fixed photosynthetic capacity, or increased photosynthetic capacity with a fixed g_c decreasing p_i and Δ. The ratio of leaf area to root area will determine the water supply per unit leaf area which will strongly determine g_c, and the division of root allocation for water versus nutrient uptake will strongly determine leaf N contents and photosynthetic capacity. Across a spatial gradient in water availability, morphological plasticity could maintain consistent leaf-level physiological relationships, or decreasing water availability could be expected to decrease g_c per unit photosynthetic capacity and decrease Δ. Increased photosynthetic capacity per unit g_c, which would also result in patterns of decreasing Δ, would be an indication of an adaptation to increase WUE with decreasing water availability.

The response of both leaf and wood Δ values to decreasing mean annual rainfall varied for each species. Neither the total change in Δ from the wet to the dry edge of the distribution of each species nor the sensitivity of Δ to changes in rainfall reflected common underlying physiological tolerances. The relative ranking of species was therefore not conserved across the species distributions, unlike observations reported for other species assemblages under varying environmental conditions (Ehleringer 1993; Sandquist et al. 1993).

Patterns of Δ with species replacements

With decreasing rainfall, the new 'xeric' species encountered did not consistently exhibit patterns of higher Δ (indicating greater ability to maintain g_c relative to photosynthetic capacity) compared to the 'mesic' species already present. The replacing species generally had lower Δ than those already present on the transect, and then maintained even lower long-term Δ as they extended into areas with lower rainfalls. An experiment in a well watered common garden found genetically determined low Δ in *Eucalyptus* species from low rainfall areas (Anderson et al. 1996). Correlations between Δ and rainfall at the sites of origin have also been for populations of a single *Eucalyptus* species in a water-limited common garden (Li et al. 2000).

The response of the zone mean Δ values to decreasing mean annual rainfall directly reflected the patterns of the responses of the individual species. The species in the wetter areas were less sensitive to decreases in rainfall than the species in the dry areas. Although species such as *E. miniata*, found at the wetter end of the transect, exhibited a shift in Δ values across its distribution similar to that of *E. odontocarpa*, found at the dry end of the transect, the slope of the response of *E. miniata* was much less than the slope of the response of *E. odontocarpa*. There was no evidence within a zone that the individual species were behaving wildly divergently, resulting in the growth-form mean describing an emergent behavior at a higher level of organization that could not be predicted from the behavior of the individual components of the system. As such, this study does not present evidence that tree species diversity is important in stabilizing ecosystem fluxes of compounds such as CO_2, H_2O, and N in response to exogenous stresses (Schulze & Mooney 1993; Schulze et al. 1998).

Patterns of Δ and mean annual rainfall

The leaf and wood Δ of the dominant Eucalypts in northern Australia decreased non-linearly in response to decreasing mean annual rainfall. This study found a stronger decline in Δ values where rainfall was between 1600 and 400 mm yr^{-1} (~1.5 ‰) than was seen by Schulze et al. (1998) (who found no change), and both studies found a threshold below which Δ values sharply declined. The pattern of Δ in the Northern Territory overstory trees is clearly different from the linear decline in community averaged Δ found in southeastern Queensland with decreasing rainfall (Stewart et al. 1995). Several other studies have found non-linear responses of Δ across rainfall gradients when the range of species sampled was limited to either a single genus or growth-form. Lajtha & Getz (1993) found that the decrease in Δ values of two New Mexican conifers only occurred at the driest end of their sampled environmental gradient. Korol et al. (1999) found little change in Δ values of *Pinus radiata* at sites with effective rainfalls greater than 750 mm yr^{-1}, and then decreases in Δ as rainfalls approached 500 mm yr^{-1}. Although the sampling pattern of Stewart et al. (1995) included a shifting ratio of growth-forms, which may have had inherently different Δ values (Brooks et al. 1997; Pate et al. 1998), it would seem unlikely that the changing ratio of growth-forms would have exactly offset non-linear responses within growth-forms.

In northwestern Australia the monsoonal climate results in highly seasonal rainfall, but the occurrence of the rainfall is regular from year to year. In southeast Queensland, by comparison, the rainfall is more evenly distributed throughout the year. In areas with highly seasonal environmental conditions, indices of water availability other than annual means are probably necessary (Walker & Langridge 1997). Patterns of evaporative demand (estimated by long-term averages of SVPD), which should influence patterns of Δ (Lloyd & Farquhar 1994), did not seem to be important in determining the patterns of Δ across the Northern Territory. Mid-afternoon SVPD and SVPD weighted by moisture availability (Comstock & Ehleringer 1992) did not correlate with the patterns in Δ values (data not shown).

The reliability of the monsoon and the concentration of the mean annual rainfall into a four month period have probably been features of the northern Australian ecosystems for the last 10 million years (Pole & Bowman 1996). The predictable summer rainfall belt, where there is virtually no winter rain, extends south to 19-20°S where rainfall is about 450 mm yr^{-1}. However, at about 16°S the rainfall regime changes from one where most of the rain comes via the direct influence of the monsoon, to one where most of the rain comes primarily as smaller, isolated convective storms (Cook & Heergeden 1997; Heerdegen & Cook 1999). Major floristic boundaries have been found at around 16°S and at about 19°S (Williams et al. 1995; Egan & Williams 1996). The 16°S floristic boundary was approximately where the species typical of the wet-end of the transect were replaced by those typical of the mid-section of the gradient. Around 16°S hummock grasses, a feature of Australian arid environment, begin to co-occur with tussock grasses (Cook & Heergeden 1997; Heerdegen & Cook 1999). The 19°S 'winter rainfall' boundary marked the transition from species characteristic of the mesic savannas to those characteristic of the xeric savannas.

Because of the reliability of the monsoon-driven rainfall north of about 16°S, the soils over much of the transect may become saturated during the wet season, and the rainfall gradient largely contributing to variation in stream-flow. The water storage in the sub-soil layers may provide an adequate water supply over much of the transect for the deep-rooted trees. Although this would explain the lack of variation in Δ at higher rainfalls, Williams et al. (1996) found parameters such as tree basal area, height, and cover all increased with mean annual rainfalls from 400 to 1800 mm yr^{-1}, showing that water availability was still determining community structure. At the wetter sites, trees could be growing to heights where internal hydraulic conductivity determines leaf water status (Ryan & Yoder 1997), so that Δ values are less closely linked to soil water availability, but this hydraulic limit to tree growth may not be a universal phenomenon (Becker, Meinzer & Wullschleger 2000), especially in angiosperms (Leavitt & Newberry 1992; Becker, Tyree & Tsuda 1999).

Sapflow and eddy-flux measurements of canopy gas exchange in the wet and dry seasons at three sites along this transect (with mean annual rainfalls of 1873, 870, and 520 mm yr^{-1}) have shown that the transpiration rates per unit ground of the overstory canopy trees are remarkably consistent along the transect between the wet and the dry seasons (O'Grady, Eamus & Hutley 1999; Hutley, O'Grady & Eamus In press). Partial leaf shedding during the dry season resulted in higher leaf-area based transpiration rates during the dry season, and the leaf-area based transpiration did not vary consistently with rainfall across the gradient, matching patterns reported for *Eucalyptus* species along other gradients (Hatton et al. 1998). Overstory leaf area index dropped from around 0.9 in the wet season at the wettest site to 0.05 at the driest site, and decreased to about 60% of the wet season values during the dry season (Hutley et al. In press).

It seems that changes in LAI offset the decreases in rainfall ameliorating the impact on stomatal conductance. The lack of pattern in Δ across the distribution of many species would indicate the trees are either shedding leaves before the onset of water stress, shedding them at similar levels of water stress, or abruptly closing the stomata at similar levels of water stress. With decreasing water availability it may be the decline in leaf life-span, rather than the length of time with partially open stomata, that is the primary indicator of plant performance and distributions. The low nutrient status of Australian soils may make it difficult for the trees to increase LAI much above 1 to 1.5 in the wet season, and there seems to be little difference in the leaf-level profit margins between fully deciduous and evergreen growth-forms (Eamus et al. 1999). Intra-annual reduction in canopy leaf area, which also occurs in the evergreen species (Williams et al. 1997), would increase the water supply to the remaining leaves and maintain Δ values. Since the strength of the Δ signal also includes the amount of assimilation occurring, there will be no signal recorded when water stress completely close the stomata. The species from the arid areas may be able to continue assimilation with partially open stomata (recording a low Δ signal), while those from the wetter areas close their stomata (recording no Δ signal). The completely dry-season deciduous *E. confertiflora* exhibited little change in Δ across its distribution in response to decreasing rainfall.

Leaf Δ versus wood Δ

Whole tissue leaf Δ values were higher than whole tissue wood Δ values in all but one species. The differences between the leaf and wood Δ values did not change across the range of most species. The hypothesis that leaf Δ values might show little response to decreasing mean annual rainfall (because the leaves were grown during a sub-annual period with little water limitation at all sites) while the wood Δ values would show a stronger response (reflecting the full annual realized production and stress) was not supported. The parallel response of leaf and wood Δ values to decreasing mean annual rainfall could be due to leaf and wood growth primarily occurring at the same time during the year (Prior, Eamus & Duff 1997; Williams et al. 1997), or due to leaf production primarily relying on reserves accumulated throughout the year. The absolute differences between the leaf and wood Δ values probably reflect differences between the species in the chemistry of the tissues (Park & Epstein 1961).

Wood Δ values were less variable within and between zones than leaf Δ values, and are therefore a better measure of plant responses over large distances where long-term integrated signals are important. The variability in the leaf samples between adjacent zones could reflect the details of the environmental conditions for the specific year of sampling. As all of the leaves from a single tree were collected from a single branch, within canopy differences (Waring & Silvester 1994) were not measured except as the differences in leaf values between trees within a zone.

Conclusion

The proposed mechanism that would maintain constant growth-form averaged Δ values with decreasing rainfall (Figure 3.1) was not found. Individual species did not show consistent and decreasing Δ values with decreasing rainfall. Replacement species did not show an increased ability to maintain stomatal conductance relative to photosynthetic capacity when compared to species at the arid edge of their distributions. Instead, xeric species often had lower Δ than co-occurring mesic species. As there were not consistent, decreasing patterns of Δ across the distributions of the species, the relative Δ values of two co-occurring species, or across the distribution of a single species, do not provide a simple measure of plant performance resulting from a relativized measure of the stomatal limitation on assimilation. The lack of clear patterns in Δ across the distributions of species limits the applicability of carbon isotope discrimination as a method of identifying the physiological tolerances of species along environmental gradients in the monsoonal tropics of Australia. The nature of the selection of plant traits in natural plant populations in response to decreasing water availability, and the impact of these characters on Δ values in either the leaf or wood tissue, is still not completely resolved, and will require measurements that distinguish the changes in photosynthetic capacity from the impacts on stomatal conductance.

3.5 Literature Cited

Anderson, J.E., Williams, J., Kriedemann, P.E., Austin, M.P. & Farquhar, G.D. (1996) Correlations between carbon isotope discrimination and climate of native habitats for diverse eucalypt taxa growing in a common garden. Australian Journal of Plant Physiology 23, 311-320.

Becker, P., Meinzer, F.C. & Wullschleger, S.D. (2000) Hydraulic limitation of tree height: a critique. Functional Ecology 14, 4-11.

Becker, P., Tyree, M.T. & Tsuda, M. (1999) Hydraulic conductances of angiosperms versus conifers: similar transport sufficiency at the whole-plant level. Tree Physiology 19, 445-452.

Brooker, M.I.H. & Kleinig, D.A. (1994) Field Guide to Eucalypts: Volume 3 Northern Australia. Inkata Press, Sydney.

Brooks, J.R., Flanagan, L.B., Buchmann, N. & Ehleringer, J.R. (1997) Carbon isotope composition of boreal plants: functional groupings of life forms. Oecologia 110, 301-311.

Comstock, J.P. & Ehleringer, J.R. (1992) Correlating genetic variation in carbon isotopic composition and complex climatic gradients. Proceedings of the National Academy of Science 89, 7747-7751.

Cook, G. & Heergeden, R. (1997) The length of the rainy season can be more important than the amount of rain for savannas in the Northern Territory. Australian Collaborative Land Evaluation Program Newsletter 6, 18-20.

Eamus, D., Myers, B., Duff, G. & Williams, R. (1999) A cost-benefit analysis of leaves of eight Australian savanna tree species of differing leaf life-span. Photosynthetica 36, 575-586.

Egan, J.L. & Williams, R.J. (1996) Lifeform distributions of woodland plant species along a moisture availability gradient in Australia's monsoonal tropics. Australian Systematic Botany 9, 205-217.

Ehleringer, J.R. (1993) Carbon and water relations in desert plants: an isotopic perspective. In: Stable Isotopes and plant carbon- water relations (J. R. Ehleringer, A. E. Hall and G. D. Farquhar), 155-172. Academic Press, New York.

Ehleringer, J.R. (1994) Variation in gas exchange characteristics among desert plants. In: Ecophysiology of photosynthesis (E.-D. Schulze and M. M. Caldwell), 361-392. Springer-Verlag, Berlin.

Ehleringer, J.R. & Cooper, T.A. (1988) Correlations between carbon isotope ratio and microhabitat in desert plants. Oecologia 76, 562-566.

Farquhar, G.D., O'Leary, M.H. & Berry, J.A. (1982) On the relationship between carbon isotope discrimination and the intercellular carbon dioxide concentration in leaves. Australian Journal of Plant Physiology 9, 121-137.

Hatton, T., Reece, P., Taylor, P. & McEwan, K. (1998) Does leaf water efficiency vary among eucalypts in water-limited environments? Tree Physiology 18, 529-536.

Heerdegen, R.G. & Cook, G.D. (1999) Redefining wetness by dryness: The duration and extent of the north Australian monsoon. In: Proceedings, 20th New Zealand Geography Conference (M. Roche, M. McKenna and P. Hesp), 139-143. New Zealand Geographical Society, Hamilton N.Z.

Hubick, K.T. & Gibson, A. (1993) Diversity in the relationship between carbon isotope discrimination and transpiration efficiency when water is limiting. In: Stable Isotopes and Plant Carbon - Water Relations (J. R. Ehleringer, A. E. Hall and G. D. Farquhar), 311-325. Academic Press, San Diego.

Hutley, L.B., O'Grady, A.P. & Eamus, D. (In press) Monsoonal influences on evapotranspiration of savanna vegetation of northern Australia. Oecologia -.

Koch, G.W., Vitousek, P.M., Steffen, W.L. & Walker, B.H. (1995) Terrestrial transects for global change research. Vegetatio 121, 53-65.

Korol, R.L., Kirschbaum, M.U.F., Farquhar, G.D. & Jeffreys, M. (1999) Effects of water status and soil fertility on the C-isotope signature in *Pinus radiata*. Tree Physiology 19, 551-562.

Lajtha, K. & Getz, J. (1993) Photosynthesis and water-use efficiency in pinyon-juniper communities along an elevation gradient in northern New Mexico. Oecologia 94, 95-101.

Lauteri, M., Scartazza, A., Guido, M.C. & Brugnoli, E. (1997) Genetic variation in photosynthetic capacity, carbon isotope discrimination and mesophyll conductance in provenances of *Castanea sativa* adapted to different environments. Functional Ecology 11, 675-683.

Leavitt, S.W. & Newberry, T. (1992) Systematics of stable-carbon isotopic differences between gymnosperm and angiosperm trees. Plant Physiol. 11, 257-262.

Li, C., Berninger, F., Koskela, J. & Sonninen, E. (2000) Drought responses of *Eucalyptus microtheca* provenances depend on seasonality of rainfall in their place of origin. Australian Journal of Plant Physiology 27, 231-238.

Lloyd, J. & Farquhar, G.D. (1994) ^{13}C discrimination during CO_2 assimilation by the terrestrial biosphere. Oecologia 99, 201-205.

Myers, B.A., Duff, G.A., Eamus, D., Fordyce, I.R., O'Grady, A. & Williams, R.J. (1997) Seasonal variation in water relations of trees of differing leaf phenology in a wet-dry tropical savanna near Darwin, northern Australia. Australian Journal of Botany 45, 225-

240.

Myers, B.A., Williams, R.J., Fordyce, I., Duff, G.A. & Eamus, D. (1998) Does irrigation affect leaf phenology in deciduous and evergreen trees of the savannas of northern Australia? Australian Journal of Ecology 23, 329-339.

O'Grady, A.P., Eamus, D. & Hutley, L.B. (1999) Transpiration increases during the dry season: patterns of tree water use in eucalypt open-forests of northern Australia. Tree Physiology 19, 591-597.

Park, R. & Epstein, S. (1961) Metabolic fractionation of C^{13} & C^{12} in plants. Plant Physiology 36, 133-138.

Pate, J.S., Unkovich, M.J., Erskine, P.D. & Stewart, G.R. (1998) Australian mulga ecosystems - ^{13}C and ^{15}N natural abundances of biota components and their ecophysiological significance. Plant, Cell and Environment 21, 1231-1242.

Pole, M.S. & Bowman, D.M.J.S. (1996) Tertiary plant fossils from Australia's 'Top End'. Australian Systematic Botany 9, 113-126.

Prior, L.D., Eamus, D. & Duff, G.A. (1997) Seasonal and diurnal patterns of carbon assimilation, stomatal conductance and leaf water potential in *Eucalyptus tetrodonta* saplings in a wet-dry savanna in northern Australia. Australian Journal of Botany 45, 241-258.

Read, J. & Farquhar, G. (1991) Comparative studies in *Nothofagus* (Fagaceae). I. Leaf carbon isotope discrimination. Functional Ecology 5, 684-695.

Ryan, M.G. & Yoder, B.J. (1997) Hydraulic limits to tree height and tree growth. BioScience 47, 235-242.

Sandquist, D.R., Schuster, W.S., Donovan, L.A., Phillips, S.L. & Ehleringer, J.R. (1993)

Differences in carbon isotope discrimination between seedlings and adults of southwestern desert perennial plants. The Southwestern Naturalist 38, 212-217.

Schulze, E.-D. & Mooney, H.A. (1993) Biodiversity and ecosystem function. Springer-Verlag, Berlin.

Schulze, E.-D., Williams, R.J., Farquhar, G.D., Schulze, W., Langridge, J., Miller, J.M. & Walker, B.H. (1998) Carbon and nitrogen isotope discrimination and nitrogen nutrition of trees along a rainfall gradient in northern Australia. Australian Journal of Plant Physiology 25, 413-425.

Stewart, G.R., Turnbull, M.H., Schmidt, S. & Erskine, P.D. (1995) ^{13}C natural abundance in plant communities along a rainfall gradient: a biological integrator of water availability. Australian Journal of Plant Physiology 22, 51-55.

Walker, B.H. & Langridge, J.L. (1997) Predicting savanna vegetation structure on the basis of plant available moisture (PAM) and plant available nutrients (PAN): a case study from Australia. Journal of Biogeography 24, 813-825.

Waring, R.H. & Silvester, W.B. (1994) Variation in foliar ^{13}C values within the crown of *Pinus radiata* trees. Tree Physiology 14, 1203-1213.

Williams, D.G. & Ehleringer, J.R. (1996) Carbon isotope discrimination in three semi-arid woodland species along a monsoon gradient. Oecologia 106, 455-460.

Williams, R.J., Cook, G.D., Braithwaite, R.W., Andersen, A.N. & Corbett, L.K. (1995) Australia's wet-dry tropics: Identifying the sensitive zones. In: Impacts of climate change on ecosystems and species: Terrestrial Ecosystems (J. C. Pernetta, R. Leemans, D. Elder and S. Humphrey), 39-65. IUCN, Gland, Switzerland.

Williams, R.J., Duff, G.A., Bowman, D.M.J. & Cook, G.D. (1996) Variation in the composition and structure of tropical savannas as a function of rainfall and soil texture along a large-scale climatic gradient in the Northern Territory, Australia. Journal of Biogeography 23, 747-756.

Williams, R.J., Myers, B.A., Muller, W.J., Duff, G.A. & Eamus, D. (1997) Leaf phenology of woody species in a north Australian topical savanna. Ecology 78, 2542-2558.

Zhang, J., Marshall, J.D. & Jaquish, B.C. (1993) Genetic differentiation in carbon isotope discrimination and gas exchange in *Pseudotsuga menziesii.* Oecologia 93, 80-87.

Zhang, J.W. & Marshall, J.D. (1995) Variation in carbon isotope discrimination and photosynthetic gas exchange among populations of *Pseudotsuga menziesii* and *Pinus ponderosa* in different environments. Functional Ecology 9, 402-412.

3.6 Tables and Figures

Table 3.1

The rank order of species mean leaf and wood Δ within each of the 33 zones (Δ decreases down the column). The species are: (A) *E. miniata*, (B) *E. tetrodonta*, (C) *E. tectifica*, (D) *E. chlorophylla*, (E) *E. confertiflora*, (F) *E. pruinosa*, (G) *E. coolabah*, (H) *E. leucophloia*, (I) *E. dichromophloia*, (J) *E. terminalis*, (K) *E. odontocarpa*, (L) *E. pachyphylla*, (M) *E. gamophylla*. The groups of species within a zone (i.e. within each column) with the same superscript were not significantly different (SNK test, $\alpha = 0.05$). The first occurrence of a species when moving from the wetter north (zone 1) to the drier south (zone 33) is highlighted with a bold letter. The last occurrence of a species is lower case.

Table 3.1

Zone:	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33
Leaf	$\mathbf{A}^{1}$ $\mathbf{B}^{1}$	A^{1} B^{2}	A^{1} $\mathbf{C}^{2}$	A^{1} C^{1} B^{1}	A^{1} $\mathbf{I}^{2}$ $\mathbf{E}^{23}$ B^{3}	C^{1} A^{1} I^{1} E^{2}	C^{1} E^{12} A^{12} I^{12} B^{2}	A^{1} I^{12} B^{12} C^{12} E^{2}	I^{1} A^{1} B^{1} $\mathbf{c}^{2}$ $\mathbf{D}^{2}$ E^{2}	I^{1} $\mathbf{F}^{1}$ D^{1} B^{1} A^{1} E^{2}	F^{1} D^{2} E^{23} $\mathbf{b}^{23}$ $\mathbf{a}^{23}$ I^{23} $\mathbf{H}^{23}$ $\mathbf{J}^{23}$ $\mathbf{G}^{3}$	$\mathbf{d}^{1}$ I^{12} J^{12} F^{12} H^{12} E^{23} G^{3}	F^{1} G^{1} H^{12} E^{12} I^{2} J^{2}	I^{1} $\mathbf{e}^{1}$ G^{1}	I^{1} F^{2} J^{2} G^{2}	F^{1} J^{12} I^{12} H^{2}	J^{1} F^{1} I^{1} G^{1} H^{1}	J^{1} I^{1} F^{1} G^{2} H^{2} $\mathbf{K}^{2}$	J^{1} $\mathbf{g}^{1}$ $\mathbf{i}^{12}$ H^{23} K^{3} F^{3}	F^{1} J^{12} $\mathbf{L}^{23}$ H^{34} K^{4}	$\mathbf{f}^{1}$ J^{1} K^{1} H^{1}	J^{1} $\mathbf{h}^{12}$ K^{12} L^{2}	J^{1} L^{1} $\mathbf{k}^{1}$	J^{1} L^{1} $\mathbf{M}^{2}$	J^{1} L^{2}	J^{1} $\mathbf{l}^{2}$	J^{1}	M^{1} J^{1}	J^{1}	J^{1}	J^{1} M^{2}	$\mathbf{j}^{1}$ M^{1}	$\mathbf{m}^{1}$
Wood	$\mathbf{A}^{1}$ $\mathbf{B}^{2}$	A^{1} B^{2}	A^{1} $\mathbf{C}^{2}$	A^{1} C^{1} B^{1}	A^{1} $\mathbf{E}^{1}$ $\mathbf{I}^{1}$ B^{1}	I^{1} A^{2} C^{2} E^{2}	I^{1} E^{1} C^{1} A^{1} B^{2}	C^{1} E^{2} A^{2} B^{2} I^{2}	$\mathbf{D}^{1}$ $\mathbf{c}^{12}$ B^{12} A^{12} E^{12} I^{2}	$\mathbf{F}^{1}$ D^{1} A^{1} I^{1} E^{1} B^{1}	D^{1} F^{1} $\mathbf{H}^{12}$ $\mathbf{b}^{12}$ E^{12} I^{23} $\mathbf{a}^{23}$ $\mathbf{G}^{23}$ $\mathbf{J}^{3}$	$\mathbf{d}^{1}$ F^{1} G^{1} I^{1} H^{1} J^{1} E^{1}	G^{1} F^{12} H^{12} E^{12} J^{12} I^{2}	$\mathbf{e}^{1}$ I^{1} G^{1}	J^{1} G^{1} F^{1} I^{1}	F^{1} H^{2} J^{3} I^{3}	F^{1} G^{1} J^{12} H^{2} I^{2}	F^{1} G^{1} I^{1} J^{1} $\mathbf{K}^{1}$ H^{1}	$\mathbf{i}^{1}$ F^{12} J^{23} $\mathbf{g}^{3}$ H^{3} K^{4}	F^{1} H^{2} J^{23} K^{23} $\mathbf{L}^{3}$	$\mathbf{f}^{1}$ H^{1} J^{1} K^{1}	L^{1} $\mathbf{h}^{12}$ J^{12} K^{2}	L^{1} J^{2} $\mathbf{k}^{3}$	L^{1} J^{1} $\mathbf{M}^{1}$	L^{1} J^{1}	$\mathbf{l}^{1}$ J^{2}	J^{1}	J^{1} M^{1}	J^{1}	J^{1}	J^{1} M^{2}	M^{1} $\mathbf{j}^{1}$	$\mathbf{m}^{1}$

Figure Legends

Figure 3.1

The hypothesized response of leaf (open symbols and dashed lines) and wood (closed symbols and solid lines) Δ of three sequentially distributed species along a gradient of decreasing rainfall. The lines connecting the symbols give the ranges of expected values for each species, and the bold lines give the growth-form average values. It is hypothesized that there will be consistent decreases in Δ across the distribution of each species reflecting the decline in the ability to maintain stomatal conductance with decreasing moisture availability. Leaf Δ will record plant responses during a narrow sub-annual optimal period when the leaves are formed (here a 2‰ decrease across the distribution of each species). Wood Δ values, integrating many annual signals of production-weighted Δ, will exhibit stronger responses than leaf Δ (here a 3‰ decreases across the distribution of each species). Species replacements are marked by an increased ability to acquire water, leading to an increased ability to maintain conductance relative to photosynthetic capacity. The growth-form average response to decreasing rainfall will mask the responses of the individual species, and will show little trend across the transect as species with higher Δ replace those with lower values, until no further replacement species are available.

Figure 3.2

(a) The predicted mean annual rainfall in the 33 zones where samples were collected (ANUCLIM 1.8, Centre for Resource and Environmental Studies, ANU). (b) The calculated annual average mid-afternoon vapor pressure deficits (closed circles), and during the wet season (open circles). (c) The sequence of species collected along the transect. The open circles denote zones with the range of the species where it could not be found. The spacing between sample locations varies because not all species co-occurred as a mixed forest within each zone.

Figure 3.3

The responses of the individual species leaf and wood Δ ($\bar{x}$ ± SE) to decreasing mean annual rainfall. Significant trends ($\alpha=0.05$) in leaf Δ are given by the dashed lines, and by the solid lines for wood Δ.

Figure 3.4

The relationship between the leaf and wood Δ values predicted from the mean annual rainfall for each of the species. The end points of the lines give the range of rainfalls where the species was sampled as diagramed in Figure 3.1.

Figure 3.5

The response of the zone mean (± SE) leaf and wood Δ values to decreasing mean annual rainfall. The regression lines from the full set of values ($n = 645$) are; leaf $\Delta = 14.29 + 18.15 * PPT_m - 17.74 * PPT_m^2 + 5.76 * PPT_m^3$ ($r^2 = 0.45$), and wood $\Delta = 13.26 + 16.88 * PPT_m - 16.28 * PPT_m^2 + 5.24 * PPT_m^3$ ($r^2 = 0.59$) when rainfall is expressed in meters (PPT_m).

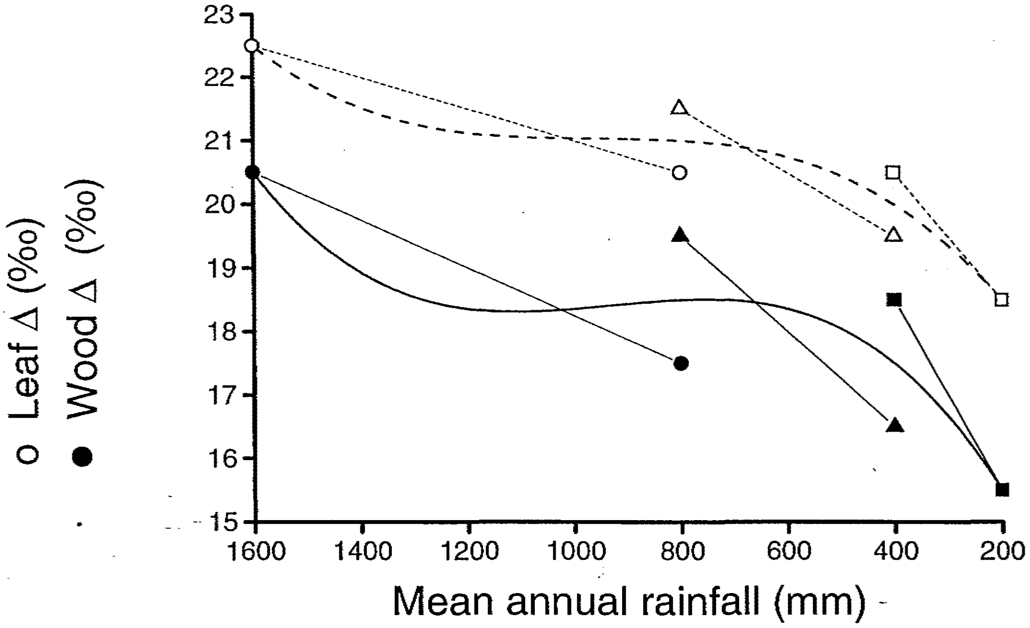

○ Leaf Δ (‰)
● Wood Δ (‰)
23
22
21
20
19
18
17
16
15
1600
1400
1200
1000
800
600
400
200
Mean annual rainfall (mm)

Figure 3.1

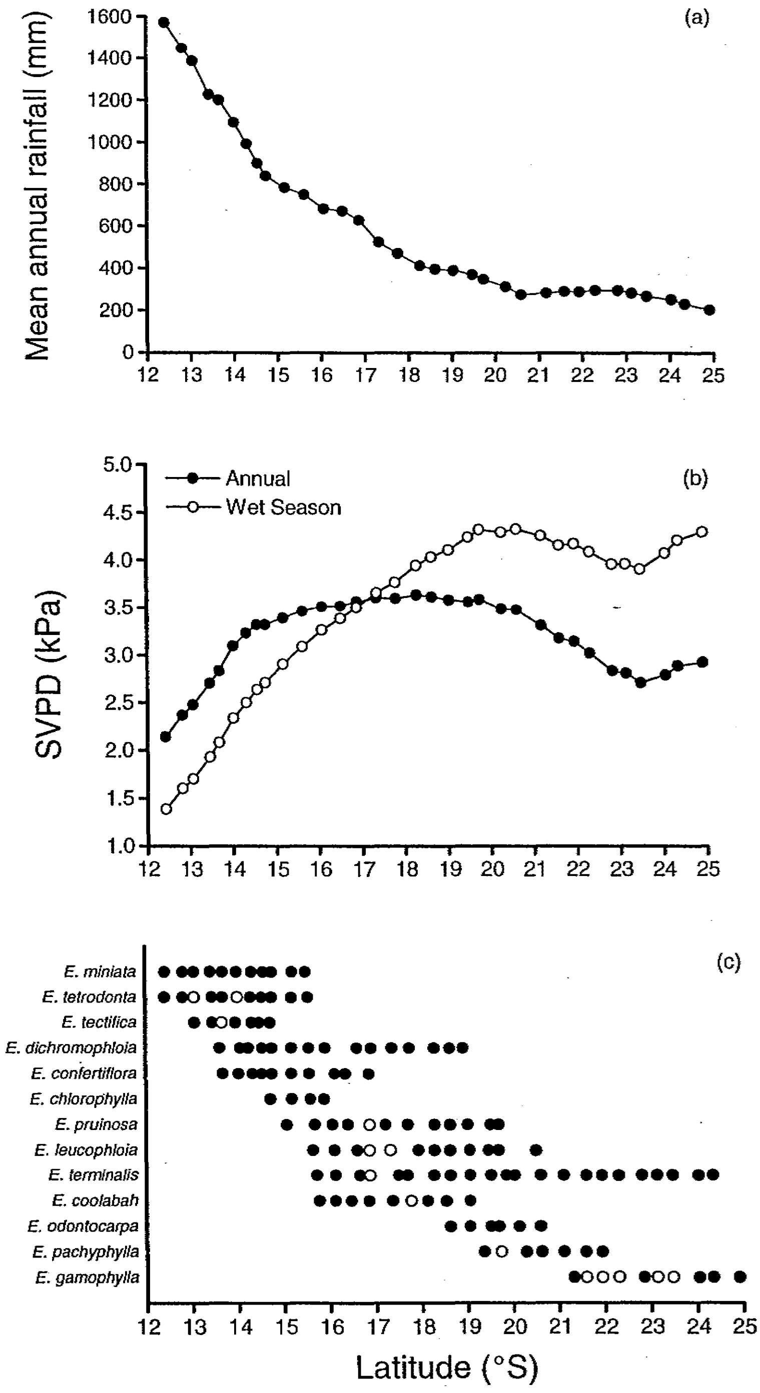
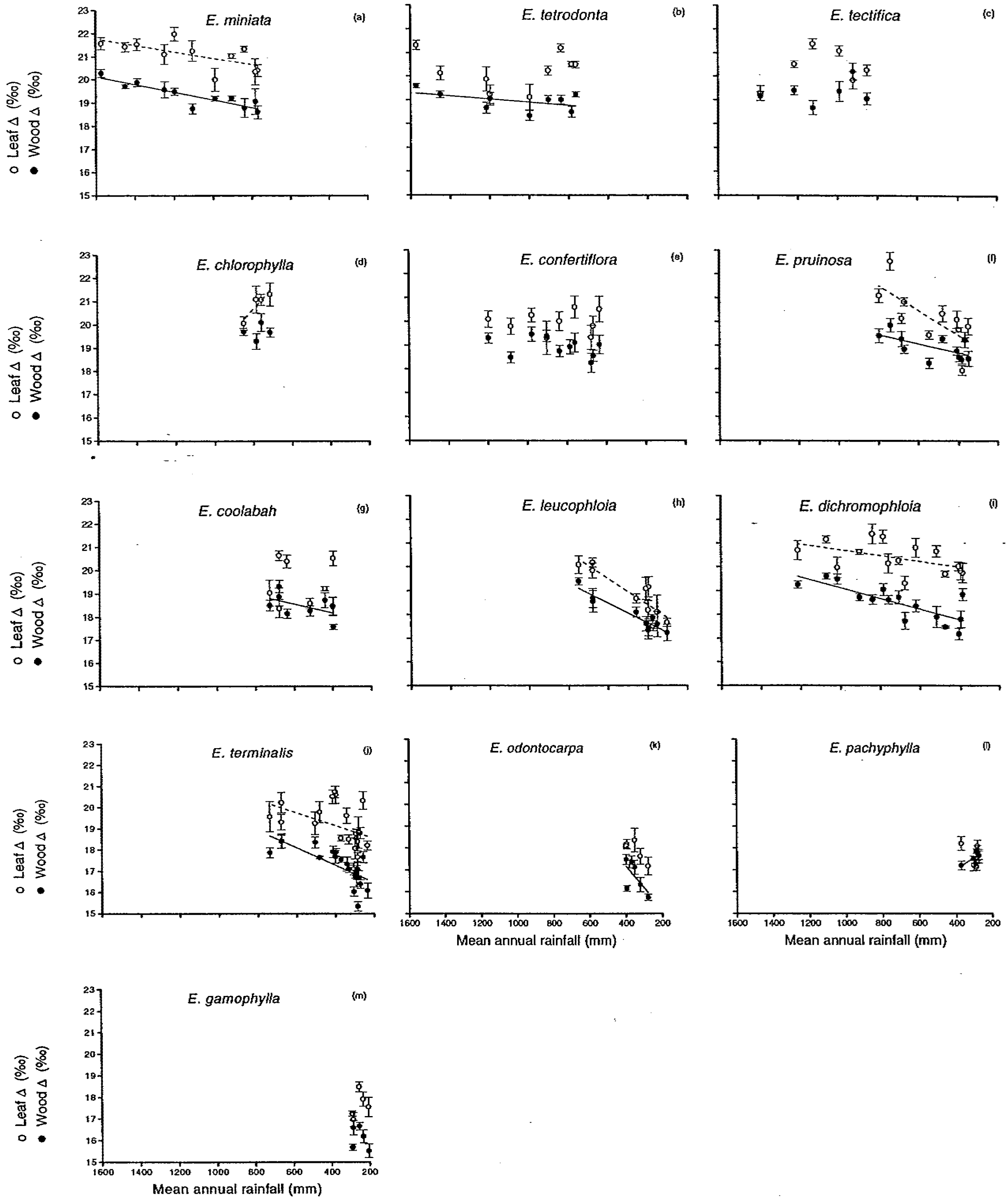

(a)
Mean annual rainfall (mm)
0
200
400
600
800
1000
1200
1400
1600
12 13 14 15 16 17 18 19 20 21 22 23 24 25
(b)
Annual
Wet Season
SVPD (kPa)
1.0
1.5
2.0
2.5
3.0
3.5
4.0
4.5
5.0
12 13 14 15 16 17 18 19 20 21 22 23 24 25
(c)
E. miniata
E. tetrodonta
E. tectifica
E. dichromophloia
E. confertiflora
E. chlorophylla
E. pruinosa
E. leucophloia
E. terminalis
E. coolabah
E. odontocarpa
E. pachyphylla
E. gamophylla
12 13 14 15 16 17 18 19 20 21 22 23 24 25
Latitude (°S)

Figure 3.2



E. miniata
(a)
E. tetrodonta
(b)
E. tectifica
(c)
E. chlorophylla
(d)
E. confertiflora
(e)
E. pruinosa
(f)
E. coolabah
(g)
E. leucophloia
(h)
E. dichromophloia
(i)
E. terminalis
(j)
E. odontocarpa
(k)
E. pachyphylla
(l)
E. gamophylla
(m)
○ Leaf Δ (‰)
● Wood Δ (‰)
23
22
21
20
19
18
17
16
15
1600
1400
1200
1000
800
600
400
200
Mean annual rainfall (mm)

Figure 3.3

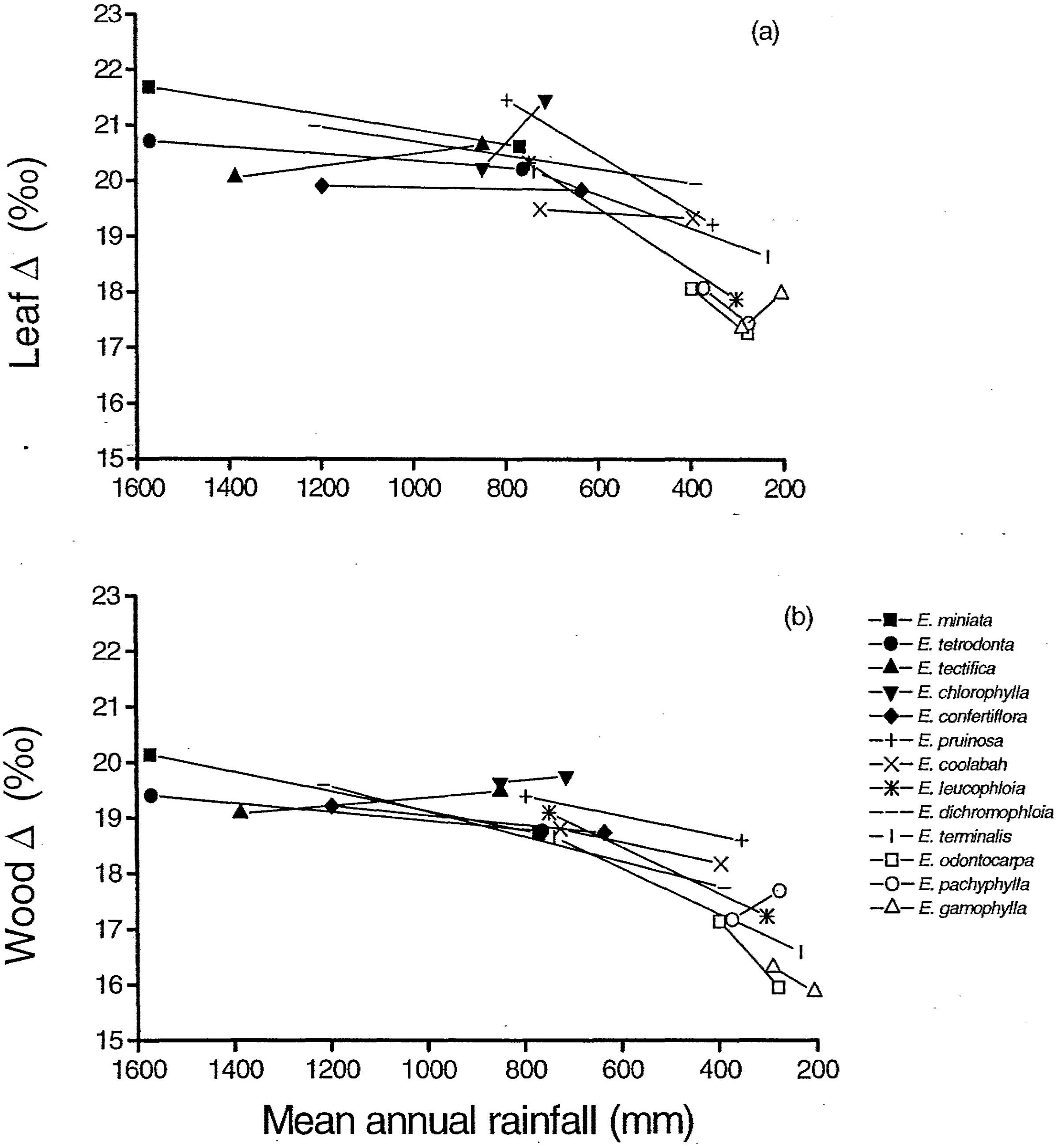

(a)
Leaf Δ (‰)
23
22
21
20
19
18
17
16
15
1600
1400
1200
1000
800
600
400
200
(b)
Wood Δ (‰)
Mean annual rainfall (mm)
E. miniata
E. tetrodonta
E. tectifica
E. chlorophylla
E. confertiflora
E. pruinosa
E. coolabah
E. leucophloia
E. dichromophloia
E. terminalis
E. odontocarpa
E. pachyphylla
E. gamophylla

Figure 3.4

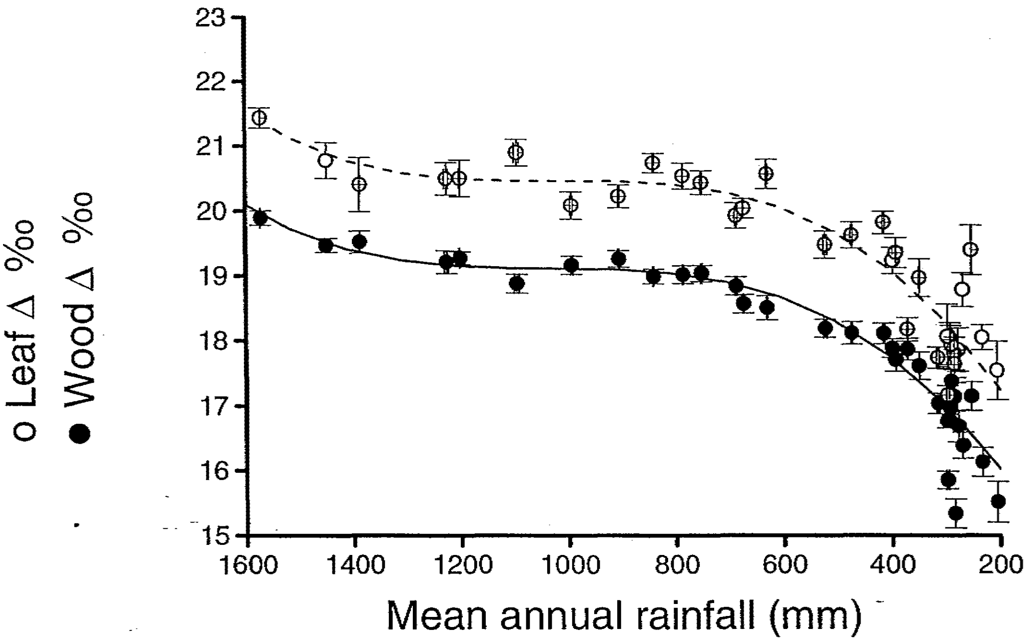

o Leaf Δ ‰
● Wood Δ ‰
23
22
21
20
19
18
17
16
15
1600
1400
1200
1000
800
600
400
200
Mean annual rainfall (mm)

Figure 3.5

Chapter 4

Resource substitution and leaf nitrogen concentrations in a sequence of *Eucalyptus* species along a rainfall gradient in the Northern Territory, Australia

Summary

1. Photosynthesis can be viewed as a two step process, with stomatal conductance in series with mesophyll conductance. Stomatal conductance depends on the plant being able to maintain the inevitable transpiration, while mesophyll conductance depends on the nitrogen investment in photosynthetic enzymes. Any decrease in either step can be offset by an equivalent increase in the other, maintaining the overall assimilation rate. This change in growth strategy is known in economics as resource substitution.
2. The area-based leaf nitrogen contents of 13 overstory *Eucalyptus* species increased with decreasing rainfall along a sub-continental rainfall gradient in the Northern Territory, Australia.
3. The mathematical treatment of resource substitution, and related issues from economics, were developed and applied to explain the observed patterns of increasing leaf nitrogen content with decreasing rainfall.
4. From the theoretical development, nitrogen-use efficiency and water-use efficiency during photosynthesis are necessarily opposed.
5. From the estimated patterns of total canopy nitrogen and annual tree transpiration flux it was possible to calculate the carbon costs of nitrogen and water use.
6. Between 50 and 75% of the change in water-use with the change in the cost of water across the rainfall gradient could be attributed to the change in nitrogen investment in the leaves (i.e. the resource substitution effect), with the remainder of the change in water use being attributable to the change in the cost of water itself.

4.1 Introduction

One of the basic tenets of plant ecophysiology is the adaptive significance of maximizing carbon uptake. A morphological or physiological trait that maintains carbon gain under decreasing resource levels should appear in many species (Mooney, Ferrar & Slatyer 1978; Grime 1979), especially in closely related species where the trait only has to appear once in a common ancestor (Harvey & Pagel 1991). These traits should be present in response to decreasing resources, regardless of the absolute resource levels, as long as they enhance carbon gain.

Many ecophysiological processes require multiple resources. In some cases the ratio of these required resources is tightly coupled, while in other cases the limitations of one resource may be offset by increased amounts of another resource (Bloom, Chapin & Mooney 1985). The efficient use of one resource may interfere with, or even oppose, the efficient use of another resource (Field, Merino & Mooney 1983).

Carbon gain depends on the ability to maintain stomatal conductance (*g*), and sustain the inevitable loss of water through transpiration, and upon the investment of nutrients, primarily nitrogen, in photosynthetic enzymes. The two requirements are in series, so that supplying CO_2 into the intercellular airspaces depends upon *g*, and the withdrawal of CO_2 during assimilation depends on the nitrogen investment. In order to maintain a constant assimilation rate, any change in either conductance or nitrogen investment needs to be offset by an equivalent and opposite change in the other. Not only are water-use efficiency and nitrogen-use efficiency (where the "efficiencies" measure the leaf level instantaneous exchanges of water for carbon, and carbon per unit nitrogen) in opposition, but when either nitrogen or water are limiting, there should be a compensatory increase in the use of the non-limiting factor.

In arid systems, where nitrogen and water uptake can be spatially decoupled, allocation for optimal return on the two independent resources could reflect plant growth strategies. In most systems, N availability and water availability are closely coupled and, to the extent that ion mobility in the soil scales with the hydraulic conductivity, are inseparable. However, in arid systems where N is mainly mineralized near the surface, while the reliable water supply is deep within the soil, the two processes, N uptake and water uptake, are separate and their costs in terms of root production in the different soil layers measurable (Pate, Jeschke & Aylward 1995; Dawson & Pate 1996). Because the processes do not co-occur, the balance between leaf N levels and g are the result of plant growth strategies and not just the N concentration of the transpiration stream.

Where there is low water availability, resulting in low leaf conductances which reduce the supply of CO_2 for photosynthesis, increased leaf nitrogen contents per unit leaf area (N_{area}) could be important in allowing plants to have higher photosynthetic capacities (A) and greater ability to remove CO_2 from the intercellular airspaces, and thus higher water-use efficiencies (see following theory development in Chapter 4.2). Limited g with high A will cause low intercellular CO_2 concentrations (c_i) and low carbon isotope discrimination (Δ) values. Patterns of decreasing Δ values have been reported across transects with decreasing mean annual rainfall at the community level (Stewart et al. 1995) and both within and between replacement species (Schulze et al. 1998; Miller, Williams & Farquhar 2001). This pattern would decrease the nitrogen-use efficiency, and should occur only when the return (increase in assimilation) on an investment for acquiring nitrogen (root growth near the soil surface) is greater than the return on an investment for acquiring water (root growth in deep soil layers).

Changes in N_{area} in response to changing levels of N or water availability, are separable issues from the carbon investment to surround the N_{area} and time required to recover the carbon investment. Higher investments in C_{area} (or leaf mass per unit area, LMA) have been proposed to decrease the vulnerability of the N_{area} to herbivory and increase the mechanical strength of the leaves in order to resist low water potentials (Mooney & Gulmon 1979; Mooney & Gulmon 1982; Cunningham, Summerhayes & Westoby 1999). Higher investments in C_{area} increase the time required to recover the costs of the carbon investment (leaf payback period) as they have no positive effect on photosynthetic capacities. Increased leaf payback periods may then require increased investment to protect against the accumulating probability of damage. In addition to the carbon return required of the displayed N_{area} determined by the C_{area} are the other components of the growth strategy of the plant such as the costs of the roots providing the nitrogen and continuing water supply, the transport tissues, and the reproductive effort. In areas with low N availability the time required to accumulate the N_{area} lost when the leaves are shed will influence the payback period. Where immobile nutrients such as phosphorus are low, the payback period will include the amount of carbon needed for root growth and soil mining.

The increases in carbon investment per unit area will increase the time required to recover the cost of the leaves if there is not a compensatory increase in photosynthetic capacity. Although the spatial display of N is an indication of photosynthetic capacity, changes in the mass-based leaf N concentrations give a better indication of the time required to recover the carbon costs supporting that nitrogen investment (Evans 1989; Field 1991). If there is a selection pressure to maintain a constant leaf payback period (as there is along the environmental gradient in this study where there is a strongly seasonal rainfall combined with decreasing mean annual rainfalls; and the rainfall seasonality influencing leaf life-spans), as LMA increases in response to water stress, the N_{area} needs to increase in order to increase the photosynthetic capacity. This could lead to N_{mass} concentrations not responding to increasing LMA.

Resource substitution is an intriguing ecological process that would maximize plant performance under multi-resource limitations, but could be difficult to quantify in naturally occurring plant populations. It would require some knowledge of both the availability of the limiting resources (i.e. N and water), and the increase in carbon gain for an investment toward acquiring each resource over the range of resource availabilities. As a first step, N_{area} and N_{mass} were measured across the distributions of a series of co-occurring and replacement *Eucalyptus* species across an 8-fold decrease in mean annual rainfall from Darwin to the southern border of the Northern Territory in Australia. These analyses were conducted on the same tissue as was used for the Δ measurements described in Chapter 3. From an understanding of the plant responses (in terms of changes in N_{area}) across their distributions along this gradient, and between replacement species, some inferences about the changes in the cost of acquiring water versus acquiring nitrogen and the plasticity of growth strategies can be made. However, the actual costs of acquiring either water or nitrogen (including the actual availability of N) were beyond the scope of this study.

The specific goals of this research were to:

1) transcribe the theory of resource substitution developed in economics into ecophysiological terms and explore the implications for the simultaneous optimal use to two resources.
2) examine the pattern of area-based leaf nitrogen concentrations (N_{area}) with decreasing mean annual rainfall, where an increase could indicate that resource substitution was occurring.
3) establish whether the mechanism for increasing N_{area} was the concentrating of leaf tissue (an increase in total leaf mass per unit area), or was the result of increasing N_{mass} with decreasing rainfall and increasing LMA.
4) document whether the changes in LMA reflected an increasing lignification of the leaves (assuming lignin has about 50% more C per unit mass than cellulose), which should be reflected in the easily measured C_{mass}.
5) investigate whether resource substitution occurs within a species (across its distribution along a gradient) or if it occurs at the community level defining species replacements, i.e. species segregate along the rainfall gradient with those with higher N_{area} occurring in drier areas.

An understanding of leaf nitrogen levels will also help explain the observed patterns of decreasing Δ with decreasing rainfall (Miller et al. 2001) which could be the result of either reduced g or adaptations to maintain g but with increased A. Tissue N concentrations in savanna vegetation are also important to know when studying the impact of fire on ecosystem N budgets (Andersen et al. 1998).

4.2 Theory

Resource substitution is a well-known phenomenon in economics, and the theory can be applied to plant eco-physiology. The economic theory describing the purchasing behavior of consumers, when there are several desired items and limited purchasing power, and of firms attempting to maximize productivity, when their product requires several components of variable cost, is well developed and described in introductory texts on the economics of firms (e.g. Thompson & Formby 1993). Some of the basic concepts include:

1) Consumer purchasing varies inversely with the cost of items and when purchasing several items, more of the cheaper items will be purchased, until all items return the same satisfaction per item purchased (i.e. that all partial derivatives of the return function are equal and zero).
2) There is a diminishing return (i.e. a decrease in consumer satisfaction) with increased purchasing (i.e. the second derivatives are negative).
3) Consumers are able to rank all combinations of goods, and these rankings are logically consistent (mathematically transitive), i.e. if the combination of goods A is ranked higher than B, and B is ranked higher than C, then A must be higher than C.
4) Higher rates of consumption are preferred over lower rates (i.e. the first derivatives are positive), and the demand function is convex, so that if a consumer is indifferent between two combinations of goods, A and B, a combination C which is the weighted average of A and B will be preferred.

These statements have equivalent interpretations for a firm producing items. A business which requires several inputs in order to construct its product will maximize profit when the return per item produced is equally limited by the incremental cost of each input. When the total capital available for investing in the required processes is fixed, a reduction in the cost of any single requirement will allow more of that capacity to be purchased and increase the overall production capacity of the firm. A classic trade-off is between the investment in the technological capability of the production facilities and labor requirements. A change in the cost of either component will shift the optimal ratio of purchasing both components and also affect the overall productivity of the firm unless there is a compensatory change in the capitalization.

Plants can either be thought of as consumers purchasing resources to maximize an undefined utility function, or as firms specifically attempting to maximize carbon uptake. In either case the ultimate goal is persistence in the gene pool as an adult generating propagules to compensate for the statistical probability of death.

If the goal of a plant is carbon gain, then the economics of plant productivity along resource gradients can be analyzed through the carbon investment necessary to supply the total canopy N content (N_t) and the carbon investment for maintaining transpiration (E_t). Changes in either the N availability in the soil, or water availability, will cause a shift in the allocation pattern of carbon between these two costs, as well as a shift in the over all productivity of the plant. A separate, but related problem is the optimal leaf area index (LAI) and the display of the N_a and E_a at a given location along a resource gradient. As the LAI increases there will be increasing levels of shading within the canopy, and decreasing carbon returns per unit N_a or E_a averaged over the whole canopy (i.e. N_t or E_t). Likewise, increasing N_a or E_a at any position within a canopy will bring diminishing returns at that specific location.

It is possible to investigate how total canopy carbon assimilation can be maximized subject to the constraint that there is a limited amount of carbon available to be invested in roots for nitrogen and water uptake, and the responses of the optimal solutions to changing resource levels by using the calculus of variations as applied to economics (Toumanoff & Nourzad 1994). Treating the canopy as a "big leaf" allows the total canopy assimilation (A_T; mol C m^{-2} {ground area} yr^{-1}) to be described as some function of the total amount of water available for transpiration (E_T; mol H_2O m^{-2} {ground area} yr^{-1}) and the total canopy nitrogen content (expressed as a turnover rate: N_T; mol N m^{-2} {ground area} yr^{-1}) , i.e.

$$A_T = A\left[E_T, N_T\right]. \qquad \text{Eq. 4.1}$$

The total cost in terms of carbon invested in roots (C_T; mol C m^{-2} {ground area} yr^{-1}) can be described as the carbon investment for the continuing water uptake and the original N uptake when the canopy was established as

$$C_T = C_E E_T + C_N N_T \qquad \text{Eq. 4.2}$$

where C_E is the cost of water uptake (mol C {in roots in the deeper soil layers} mol^{-1} H_2O) and C_N is the cost of nitrogen uptake (mol C {in roots in the shallower soil layers} mol^{-1} N).

The diminishing returns for increasing E_T and N_T can be found from the slopes of the functions defining the marginal products of water and nitrogen (MP_E and MP_N), where the

$$MP_E = {\partial A_T}/{\partial E_T} \qquad \text{Eq. 4.3}$$

and the

$$MP_N = {\partial A_T}/{\partial N_T} \qquad \text{Eq. 4.4}$$

such that

$$MP_E = {\partial A}/{\partial E_T} \qquad \text{Eq. 4.5}$$

and

$$MP_N = {\partial A}/{\partial N_T}\,. \qquad \text{Eq. 4.6}$$

The responsiveness of A_T to changes in E_T and N_T can be measured by the elasticities of demand, i.e.

$$\varepsilon_{AE} = \frac{\partial A_T}{\partial E_T}\frac{E_T}{A_T} \qquad \text{Eq. 4.7}$$

and

$$\varepsilon_{AN} = \frac{\partial A_T}{\partial N_T}\frac{N_T}{A_T} \qquad \text{Eq. 4.8}$$

which have the benefit of being unitless and therefore directly comparable.

The canopy assimilation function, $A[E_T,N_T]$, describes a surface of potential A_T values reflecting all possible $\{E_T, N_T\}$ combinations, rather than just the observed sequence of paired values (Figure 4.1). Contour intervals on the surface reflect $\{E_T, N_T\}$ combinations that yield a constant total assimilation, A_{T*}, and are called indifference curves when describing consumer behavior or isoquants when describing inputs of a production function. An isoquant at a specific value of $A_T = A_{T*}$ is therefore implicitly defined as

$$I\left[E_T, N_T\right] \equiv A_{T*} - A\left[E_T, N_T\right] = 0. \qquad \text{Eq. 4.9}$$

Movement along an isoquant reflects the changing ratio of the required inputs which can be measured by the marginal rate of technical substitution (*MRTS*). The change in N_T with a change in E_T that yields the same A_T is

$$\frac{dN_T}{dE_T} = -\frac{\partial A / \partial E_T}{\partial A / \partial N_T} = -\frac{MP_E}{MP_N} = -MRTS_{EN} \qquad \text{Eq. 4.10}$$

and the change in E_T required by a change in N_T is

$$\frac{dE_T}{dN_T} = -\frac{\partial A / \partial N_T}{\partial A / \partial E_T} = -\frac{MP_N}{MP_E} = -MRTS_{NE}. \qquad \text{Eq. 4.11}$$

Equation 4.2 can be used to find an isocost line of $\{E_T, N_T\}$ combinations that have equal costs by setting $C = C_{T*}$, which then allows N_T to be expressed as a function of E_T, the total carbon available for root growth, and the costs of acquiring water and nitrogen as

$$N_T = \frac{C_{T*}}{C_N} - \frac{C_E}{C_N} E_T. \qquad \text{Eq. 4.12}$$

The observed changes in N_T with changes in E_T can be used to find the ratio of C_E to C_N since differentiating Equation 4.12 yields

$$\frac{dN_T}{dE_T} = -\frac{C_E}{C_N}. \qquad \text{Eq. 4.13}$$

Alternatively, the total derivative of the cost function (Equation 4.2) can be found as

$$dC_T = \frac{\partial C_T}{\partial E_T} dE_T + \frac{\partial C_T}{\partial N_T} dN_T, \qquad \text{Eq. 4.14}$$

which along an isocost line equals 0, and can then be rearranged into Equation 4.14 since $\partial C_{\mathrm{T}} / \partial E_{\mathrm{T}} = C_{\mathrm{E}}$ and $\partial C_{\mathrm{T}} / \partial N_{\mathrm{T}} = C_{\mathrm{N}}$.

The lowest total cost along an isoquant occurs when an isocost function is tangent such that Equations 4.10 and 4.13 are equal (Figure 4.2). When this happens, the cost minimizing combination of inputs has a ratio of costs equal to the inverse ratio of their marginal products and the marginal rate of technical substitution, i.e.

$$\frac{C_{\mathrm{E}}}{C_{\mathrm{N}}} = \frac{MP_{\mathrm{N}}}{MP_{\mathrm{E}}} = MRTS_{\mathrm{NE}} \qquad \text{Eq. 4.15}$$

As resource levels change, the cost of their acquisition changes (Figure 4.3). A decrease in the cost of a single input will allow more of it to be used, and therefore an increase in productivity without increasing costs. Less of the more expensive resource can also be used, allowing yet again more of the cheaper resource to be used. The former change in resource use is described as an income effect, since the decrease in costs is effectively an increase in real income, while the later is the substitution effect which results in a change in resource use due only to a change in the ratio of inputs without a change in productivity.

The dynamics of the optimal patterns of resource use along resource gradients can be explored as follows in a simplified system with two inputs, nitrogen and water. Along the gradient the optimal values of E_{T} and N_{T} can be found by solving the three derivatives of the Lagrangian function (or performance index) which combines the production function (Equation 4.1) and the cost constraint (Equation 4.2)

$$J[E_{\mathrm{T}}, N_{\mathrm{T}}, \lambda] = A[E_{\mathrm{T}}, N_{\mathrm{T}}] + \lambda(C_{\mathrm{T}} - C_{\mathrm{E}}E_{\mathrm{T}} - C_{\mathrm{N}}N_{\mathrm{T}}) \qquad \text{Eq. 4.16}$$

which are

$$\partial J / \partial E_{\mathrm{T}} = \partial A / \partial E_{\mathrm{T}} - \lambda C_{\mathrm{E}} = 0 \text{ ,} \qquad \text{Eq. 4.17}$$

$$\partial J / \partial N_{\mathrm{T}} = \partial A / \partial N_{\mathrm{T}} - \lambda C_{\mathrm{N}} = 0 \text{, and} \qquad \text{Eq. 4.18}$$

$$\partial J / \partial \lambda = C_{\mathrm{T}} - C_{\mathrm{N}}N_{\mathrm{T}} - C_{\mathrm{E}}E_{\mathrm{T}} = 0 \qquad \text{Eq. 4.19}$$

for the three unknowns (E_T, N_T, and λ). Checking that the solution is a maximum rather than a minimum can be done by checking that the determinant of the bordered Hessian matrix (H_B, comprising all possible second derivations of Equations 4.17 to 4.19) is positive, i.e.

$$|H_B| = \begin{vmatrix} \partial^2 J / \partial E_T \partial E_T & \partial^2 J / \partial E_T \partial N_T & \partial^2 J / \partial E_T \partial \lambda \\ \partial^2 J / \partial N_T \partial E_T & \partial^2 J / \partial N_T \partial N_T & \partial^2 J / \partial N_T \partial \lambda \\ \partial^2 J / \partial \lambda \partial E_T & \partial^2 J / \partial \lambda \partial N_T & \partial^2 J / \partial \lambda \partial \lambda \end{vmatrix} = \begin{vmatrix} \partial^2 A / \partial E_T \partial E_T & \partial^2 A / \partial E_T \partial N_T & -C_E \\ \partial^2 A / \partial N_T \partial E_T & \partial^2 A / \partial N_T \partial N_T & -C_N \\ -C_E & -C_N & 0 \end{vmatrix} > 0$$

Eq. 4.20

The introduced parameter, λ, measures the effect on the maximal A_T^* with changes in total carbon available for root growth, i.e.

$$\lambda^* = \partial A_T^* / \partial C_T$$ Eq. 4.21

where

$$A_T^* = A[E_T^*, N_T^*]$$ Eq. 4.22

and is the maximal total canopy carbon gain using the values of E_T, N_T, and λ which are optimal. These optimal values (E_T^*, N_T^*, and λ^*) depend upon the costs of acquiring nitrogen and water, and the total available carbon and are therefore the functions;

$$N_T^* = N^*[C_E, C_N, C_T],$$ Eq. 4.23

$$E_T^* = E^*[C_E, C_N, C_T],$$ Eq. 4.24

and $\lambda^* = \lambda^*[C_E, C_N, C_T]$. Eq. 4.25

The behavior of the optimal solutions under changing environmental conditions, which affect the costs of acquiring nitrogen, water, and the total available carbon for investing in roots, can be explored by substituting Equations 4.23 through 4.25 into Equations 4.17 to 4.19 creating the identities;

$$\partial A\left[N^*\left[C_E, C_N, C_T\right], E^*\left[C_E, C_N, C_T\right]\right] \Big/ \partial E_T - \lambda^*\left[C_E, C_N, C_T\right] C_E \equiv 0 \qquad \text{Eq. 4.26}$$

$$\partial A\left[N^*\left[C_E, C_N, C_T\right], E^*\left[C_E, C_N, C_T\right]\right] \Big/ \partial N_T - \lambda^*\left[C_E, C_N, C_T\right] C_N \equiv 0 \qquad \text{Eq. 4.27}$$

$$C_T - C_N N^*\left[C_E, C_N, C_T\right] - C_E E^*\left[C_E, C_N, C_T\right] \equiv 0 \qquad \text{Eq. 4.28}$$

and then differentiating against C_E, C_N, or C_T. The responses along a rainfall gradient with changing costs of water are (using the chain rule);

$$\partial^2 A \big/ \partial E_T \partial E_T \; \partial E^* \big/ \partial C_E + \partial^2 A \big/ \partial E_T \partial N_T \; \partial N^* \big/ \partial C_E - C_E \, \partial \lambda^* \big/ \partial C_E = \lambda^* \qquad \text{Eq. 4.29}$$

$$\partial^2 A \big/ \partial N_T \partial E_T \; \partial E^* \big/ \partial C_E + \partial^2 A \big/ \partial N_T \partial N_T \; \partial N^* \big/ \partial C_E - C_N \, \partial \lambda^* \big/ \partial C_E = 0 \qquad \text{Eq. 4.30}$$

$$- C_E \, \partial E^* \big/ \partial C_E - C_N \, \partial N^* \big/ \partial C_E + 0 \, \partial \lambda^* \big/ \partial C_E = E^* \qquad \text{Eq. 4.31}$$

or

$$\begin{bmatrix} \partial^2 A \big/ \partial E_T \partial E_T & \partial^2 A \big/ \partial E_T \partial N_T & - C_E \\ \partial^2 A \big/ \partial E_T \partial E_T & \partial^2 A \big/ \partial N_T \partial N_T & - C_N \\ - C_E & - C_N & 0 \end{bmatrix} \begin{bmatrix} \partial E^* \big/ \partial C_E \\ \partial N^* \big/ \partial C_E \\ \partial \lambda^* \big/ \partial C_E \end{bmatrix} = \begin{bmatrix} \lambda^* \\ 0 \\ E^* \end{bmatrix} \qquad \text{Eq. 4.32}$$

when expressed as matrices. The matrix of coefficients is the bordered Hessian in Equation 4.20. The unknowns can be found using Cramer's rule from;

$$\partial E^* \big/ \partial C_E = \frac{\begin{vmatrix} \lambda^* & \partial^2 A \big/ \partial E_T \partial N_T & - C_E \\ 0 & \partial^2 A \big/ \partial N_T \partial N_T & - C_N \\ E^* & - C_N & 0 \end{vmatrix}}{\left| H_B \right|} \qquad \text{Eq. 4.33}$$

$$\partial N^* / \partial C_{\mathrm{E}} = \frac{\begin{vmatrix} \partial^2 A / \partial E_{\mathrm{T}} \partial E_{\mathrm{T}} & \lambda^* & -C_{\mathrm{E}} \\ \partial^2 A / \partial N_{\mathrm{T}} \partial E_{\mathrm{T}} & 0 & -C_{\mathrm{N}} \\ -C_{\mathrm{E}} & E^* & 0 \end{vmatrix}}{|H_{\mathrm{B}}|} \qquad \text{Eq. 4.34}$$

$$\partial \lambda^* / \partial C_{\mathrm{E}} = \frac{\begin{vmatrix} \partial^2 A / \partial E_{\mathrm{T}} \partial E_{\mathrm{T}} & \partial^2 A / \partial E_{\mathrm{T}} \partial N_{\mathrm{T}} & \lambda^* \\ \partial^2 A / \partial N_{\mathrm{T}} \partial E_{\mathrm{T}} & \partial^2 A / \partial N_{\mathrm{T}} \partial N_{\mathrm{T}} & 0 \\ -C_{\mathrm{E}} & -C_{\mathrm{N}} & \mathrm{E}^* \end{vmatrix}}{|H_{\mathrm{B}}|} \qquad \text{Eq. 4.35}$$

Expanding the determinant in the numerator of Equation 4.33 by the first column yields

$$\partial E^* / \partial C_{\mathrm{E}} = -\lambda^* \frac{C_{\mathrm{N}}^2}{|H_{\mathrm{B}}|} + E^* \frac{C_{\mathrm{E}}\, \partial^2 A / \partial N \partial N - C_{\mathrm{N}}\, \partial^2 A / \partial E \partial N}{|H_{\mathrm{B}}|} \qquad \text{Eq. 4.36}$$

which can be shown to also be

$$\partial E^* / \partial C_{\mathrm{E}} = -\lambda^* \frac{C_{\mathrm{N}}^2}{|H_{\mathrm{B}}|} - E^* \, \partial E^* / \partial C_{\mathrm{T}} \qquad \text{Eq. 4.37}$$

a form of the solution known as the Slutsky equation (Toumanoff & Nourzad 1994). In the Slutsky equation the substitution effect, due to a change in the cost ratio with a change in the cost of one factor (i.e. a change in C_{E}), is given by

$$-\lambda^* \frac{C_{\mathrm{N}}^2}{|H_{\mathrm{B}}|} \qquad \text{Eq. 4.38}$$

and the output effect (i.e. the change resulting from the change in A_{T} which causes a change in the total carbon available for root allocation) is given by

$$- E^{*} \, {}^{\partial E^{*}}\!/_{\partial C_{\mathrm{T}}} \, . \qquad \text{Eq. 4.39}$$

The responsiveness of a dependent variable to changes of an independent variable is measured by its elasticity as

$$\varepsilon_{xy} = \frac{\text{percentage change in } x}{\text{percentage change in } y} = \frac{dx}{dy}\frac{y}{x} \qquad \text{Eq. 4.40}$$

so the elasticity of substitution, measuring the degree of substitutability of two inputs at points along an isoquant, is given by

$$\sigma = \frac{d\left(\dfrac{N_{\mathrm{T}}}{E_{\mathrm{T}}}\right)}{d\left(\dfrac{{}^{\partial A_{\mathrm{T}}}\!/_{\partial E_{\mathrm{T}}}}{{}^{\partial A_{\mathrm{T}}}\!/_{\partial N_{\mathrm{T}}}}\right)} \frac{\dfrac{{}^{\partial A_{\mathrm{T}}}\!/_{\partial E_{\mathrm{T}}}}{{}^{\partial A_{\mathrm{T}}}\!/_{\partial N_{\mathrm{T}}}}}{\dfrac{N_{\mathrm{T}}}{E_{\mathrm{T}}}} \qquad \text{Eq. 4.41}$$

which can be implemented as

$$\sigma = - \frac{{}^{\partial A_{\mathrm{T}}}\!/_{\partial E_{\mathrm{T}}} \, {}^{\partial A_{\mathrm{T}}}\!/_{\partial N_{\mathrm{T}}} \left({}^{\partial A_{\mathrm{T}}}\!/_{\partial E_{\mathrm{T}}} \, E_{\mathrm{T}} + {}^{\partial A_{\mathrm{T}}}\!/_{\partial N_{\mathrm{T}}} \, N_{\mathrm{T}} \right)}{E_{\mathrm{T}} N_{\mathrm{T}} \left(\left({}^{\partial A_{\mathrm{T}}}\!/_{\partial N_{\mathrm{T}}} \right)^{2} {}^{\partial^{2} A_{\mathrm{T}}}\!/_{\partial E_{\mathrm{T}} \partial E_{\mathrm{T}}} - 2 \, {}^{\partial A_{\mathrm{T}}}\!/_{\partial E_{\mathrm{T}}} \, {}^{\partial A_{\mathrm{T}}}\!/_{\partial N_{\mathrm{T}}} \, {}^{\partial^{2} A_{\mathrm{T}}}\!/_{\partial E_{\mathrm{T}} \partial N_{\mathrm{T}}} + \left({}^{\partial A_{\mathrm{T}}}\!/_{\partial E_{\mathrm{T}}} \right)^{2} {}^{\partial^{2} A_{\mathrm{T}}}\!/_{\partial N_{\mathrm{T}} \partial N_{\mathrm{T}}} \right)}$$

.

Eq. 4.42

The sign of the solution of Equation 4.34 determines if the two inputs are described as competitive factors of production (when the solution is positive), or cooperative factors of production (when the solution is negative). Competitive factors compete to perform similar tasks and when more of one factor is used the marginal product of the other is decreased. Cooperative factors perform complementary tasks and when more of one factor is used the marginal product of the other is increased.

The signs of the solutions to the partial derivatives

$$\partial E^* / \partial C_T \qquad \text{Eq. 4.43}$$

and

$$\partial N^* / \partial C_T \qquad \text{Eq. 4.44}$$

can be used to determine if the resources are "normal goods" for which consumption increases with the ability to purchase them (and the solution is positive), or if they are "inferior goods" where consumption decreases with the ability to purchase them (and the solution is negative).

A simple version of the canopy assimilation function (Equation 4.1) can be developed by combining a supply model for photosynthesis,

$$A = \frac{g}{1.6}(c_a - c_i) \qquad \text{Eq. 4.45}$$

with a simple representation of the demand model,

$$A = k(c_i - \Gamma) \qquad \text{Eq. 4.46}$$

(where g is the conductance to water vapor, c_a and c_i are the ambient and internal CO_2 concentrations, k is the carboxylation efficiency, and Γ is the CO_2 compensation point) which states that assimilation is linearly related in intercellular CO_2 concentrations (as in the Rubisco limited phase) to yield

$$A = (c_a - \Gamma)\frac{g\,k}{g + 1.6\,k} \qquad \text{Eq. 4.47}$$

which, if k is understood to be $\partial A / \partial c_i$ (see Farquhar, Buckley & Miller 2002), can be expanded to include the full dynamics of more sophisticated photosynthesis models (Buckley, Miller & Farquhar 2002). For this exercise k is simply related to the leaf nitrogen content (per unit area: N_a) as

$$k = f N_a \qquad \text{Eq. 4.48}$$

and g is related to E_a as

$$E = g\,D \qquad \text{Eq. 4.49}$$

where D is the vapor pressure deficit. A_a and E_a are both per unit leaf area and can be converted to canopy totals per unit ground area (A_T, E_T, and N_T) by multiplying by the leaf area index (LAI) so that Equation 4.47 becomes

$$A_T[E_T, N_T] = (c_a - \Gamma)\frac{E_T f N_T}{E_T + 1.6\, D f N_T} \qquad \text{Eq. 4.50}$$

which describes a surface which increases asymptotically with both increasing E_T and N_T (Figure 4.1). Contour lines on the surface describe equivalent combinations of total canopy nitrogen and water use that result in the same total canopy carbon gain.

The simple canopy assimilation model (Equation 4.50) allows the performance index (Equation 4.16) to become

$$J[E_T, N_T, \lambda] = (c_a - \Gamma)\frac{E_T f N_T}{E_T + 1.6\, D f N_T} + \lambda(C_T - E_T\, C_E - N_T\, C_N) \qquad \text{Eq. 4.51}$$

and its derivatives are

$$\partial J/\partial E_T = (c_a - \Gamma)\frac{1.6 D f^2 N_T^2}{(E_T + 1.6 D f N_T)^2} - \lambda C_E = \mathrm{MP_W} - \lambda C_E\,, \qquad \text{Eq. 4.52}$$

$$\partial J/\partial N_T = (c_a - \Gamma)\frac{f E_T^2}{(E_T + 1.6 D f N_T)^2} - \lambda C_N = \mathrm{MP_N} - \lambda C_N \qquad \text{Eq. 4.53}$$

and

$$\partial J/\partial \lambda = C_T - E_T\, C_E - N_T\, C_N\,. \qquad \text{Eq. 4.54}$$

Equations 4.52 through 4.54 can be solved for the optimal values of E_T and N_T as functions of the carbon costs of water and nitrogen acquisition and the total available carbon, or C_E, C_N, and λ can be found from E_T and N_T which are easier to measure as

$$C_E = \frac{1.6 D f N_T C_T}{E_T(E_T + 1.6 D f N_T)} \qquad \text{Eq. 4.55}$$

$$C_N = \frac{E_T C_T}{N_T(E_T + 1.6 D f N_T)} \qquad \text{Eq. 4.56}$$

and

$$\lambda = (c_a - \Gamma)\frac{E_T f N_T}{C_T(E_T + 1.6 D f N_T)}. \qquad \text{Eq. 4.57}$$

The bordered Hessian of Equation 7 is

$$H_B = \begin{bmatrix} -2(c_\mathrm{a}-\Gamma)\dfrac{1.6Df^2N_\mathrm{T}^2}{\left(\mathrm{E_T}+1.6DfN_\mathrm{T}\right)^3} & 2(c_\mathrm{a}-\Gamma)\dfrac{1.6DE_\mathrm{T}f^2N_\mathrm{T}}{\left(\mathrm{E_T}+1.6DfN_\mathrm{T}\right)^3} & -C_\mathrm{E} \\ 2(c_\mathrm{a}-\Gamma)\dfrac{1.6DE_\mathrm{T}f^2N_\mathrm{T}}{\left(\mathrm{E_T}+1.6DfN_\mathrm{T}\right)^3} & -2(c_\mathrm{a}-\Gamma)\dfrac{1.6Df^2E_\mathrm{T}^2}{\left(\mathrm{E_T}+1.6DfN_\mathrm{T}\right)^3} & -C_\mathrm{N} \\ -C_\mathrm{E} & -C_\mathrm{N} & 0 \end{bmatrix} \qquad \text{Eq. 4.58}$$

which allows the Slutsky equation (Equation 4.37) separating the resource substitution and output effects to be calculated as

$$\partial E^*/\partial C_E = -\lambda\frac{C_\mathrm{N}^2\left(E_\mathrm{T}-1.6DfN_\mathrm{T}\right)^3}{2\left(c_\mathrm{a}-\Gamma\right)1.6Df^2\left(C_\mathrm{E}E_\mathrm{T}+C_\mathrm{N}N_\mathrm{T}\right)^2} - E^*\frac{E_\mathrm{T}}{\left(C_\mathrm{E}E_\mathrm{T}+C_\mathrm{N}N_\mathrm{T}\right)} \qquad \text{Eq. 4.59}$$

By applying these economic analyses to the observed patterns of leaf nitrogen content along a gradient of available water supply, as will be done in Chapter 4.5, it should be possible to explore the importance of these dynamics. Changes in growth strategy across the distribution of a single species, and across a series of replacement species, may give insight into the environmental controls of the distributions of the species.

4.3 Methods

Sampling was conducted along the Stuart Highway between Darwin (12½ °S) and the southern border of the Northern Territory (~ 25°S) as described in detail in Chapter 3 and Miller et al. (2001). The key points of the sampling procedure are summarized here again.

The 1750km distance was divided into 33 zones (each about 50 km long). The species of interest that occurred in each zone were sampled once per zone at locations where they were locally abundant. Not all possible species within a zone co-occurred at exactly the same location in a mixed forest, so samples were collected at a total of 97 locations. Most of the locations were flat, and variations in edaphic conditions were controlled for only to the extent that sampling locations were chosen where individuals of the species of interest were abundant. Sampling locations were therefore restricted to loams and sandy soils, as the species of interest were not common on clay soils. Sampling was conducted at locations accessible from the highway at the end of the dry season between 16 September and 18 October 1996.

The species were selected based on their distribution (Brooker & Kleinig 1994) to include; *E. miniata* A.Cunn. Ex Schauer, *E. tetrodonta* F.Muell., and *E. tectifica* F.Muell. which are restricted to the wetter northern end of the transect, *E. chlorophylla* Brooker&Done, *E. confertiflora* F.Muell., *E. pruinosa* Schauer, *E. coolabah* Blakely&Jacobs subsp. *coolabah*, *E. leucophloia* Brooker subsp. *QQ*, and *E. dichromophloia* F.Muell. which are found in the middle of the transect, and *E. terminalis* F.Muell., *E. odontocarpa* F.Muell., *E. pachyphylla* F.Muell., and *E. gamophylla* F.Muell. which are restricted to the drier southern end of the transect. *E. confertiflora* is completely dry-season deciduous, while the other species have varying amounts of leaf area reduction during the dry season. Adult *E. confertiflora* and *E. pruinosa* retain the juvenile leaf form, while the other species switch to the adult leaf form at maturity. *E. odontocarpa*, *E. pachyphylla*, and *E. gamophylla* are multi-stemmed mallee shrubs, while the other species are single stemmed trees.

Five individuals of each species were sampled within each zone. Ten sun-exposed leaves from the upper part of the canopy were collected from each individual. Each of the ten leaves had a hole punched and these ten samples of known area were dried and weighed together to determine the leaf mass per unit area for that individual. The ten leaves from a single individual were then ground together and combined for chemical analysis.

Leaf material was air dried in the field and re-dried to a constant weight at 80°C back in the laboratory. Samples were finely ground in either a cyclone mill or, if the samples were very small, in a ball mill. Elemental analysis (%N and %C) was done with a Carlo Erba (Milano) elemental analyzer. Repeated measures of the standard (glucosamine) and several *Eucalyptus* leaf tissue samples had standard deviations of around 0.15% for both nitrogen and carbon.

From the GPS positions recorded in the field and the elevations predicted from a digital elevation map of Australia, mean annual rainfall was predicted for the 97 locations where sampling occurred using ANUCLIM 1.8 (Centre for Resource and Environmental Studies, ANU). Statistical analyses, comprising linear regressions and ANOVA's followed by multiple range tests, were made using SAS (6.12: SAS Institute Inc.) and Microcal Origin 5.0.

4.4 Results

Mean annual rainfall decreased from about 1600 mm yr^{-1} at the northern edge of the transect to about 200 mm yr^{-1} at the southern edge of the transect (Figure 4.4a). The decrease in mean annual rainfall was non-linearly related to increasing latitude. Rainfall dropped from 1600 to 800 mm yr^{-1} between 12 and 15 °S, and from 300 to 200 mm yr^{-1} between 20 and 25 °S. Around 80% of the rain occurs during the months of December to March in the northern half of the transect (north of 18½°S). As latitude increases the rainfall becomes less seasonal, and at the southern edge of the transect only 50% of the rainfall occurs during the wet-season. During the months of June through September the area north of approximately 16½°S receives less than 2% of the mean annual rainfall, while at the southern edge of the transect 20% of the rainfall occurs during these months.

E. miniata and *E. tetrodonta* are the co-dominant species defining many of the vegetation types north of around 15°S along this transect (Figure 4.4b). *E. tectifica* and *E. chlorophylla* are two very similar appearing species with narrow, non-overlapping distributions. Their limited ranges, especially in the case of *E. chlorophylla* which was found in only four zones, made accurately representing trends across their distribution difficult. The differences between the two species, which would explain their disjunct distributions, were not clear. *E. confertiflora* was the only completely dry-season deciduous species sampled. Only extremely young leaves were available to be sampled in the middle of the distribution of the species, and they had distinctive N_{mass} values. *E. pruinosa*, *E. coolabah*, and *E. leucophloia* were three species distributed primarily in the center of the transect, from around 15 to 21°S. *E. pruinosa* and *E. leucophloia* were sampled over wide latitudinal ranges (between 4½ and 5½° latitude), and *E. coolabah* was sampled over an intermediate range (between 2½ and 3½° latitude). The combined distributions of *E. dichromophloia* and *E. terminalis* covered over 90% of the entire transect, with *E. terminalis* being present in all but the wettest 15% of the 33 sampled zones. The three multi-stemmed shrubs *E. odontocarpa*, *E. pachyphylla*, and *E. gamophylla* were restricted to the drier, southern end of the transect. The three species had the highest LMA values of the sampled *Eucalyptus* species.

As mean annual rainfall decreased across each of the distributions of the evergreen tree species, those species at the arid southern end of the transect (*E. pruinosa*, *E. coolabah*, *E. leucophloia*, *E. dichromophloia*, and *E. terminalis*) exhibited patterns of increasing N_{area} (Figure 4.5). The N_{area} values of the evergreen trees at the wetter northern end of the transect (*E. miniata*, *E. tetrodonta*, *E. tectifica*, and *E. chlorophylla*), the drought deciduous species (*E. confertiflora*), and the three mallee shrubs (*E. odontocarpa*, *E. pachyphylla*, and *E. gamophylla*) did not change as mean annual rainfall declined across the distributions of each species.

The lowest N_{area} values were found in a group of four species that were not significantly different (SNK test: Table 4.1); *E. confertiflora* followed by *E. miniata*, *E. tetrodonta*, and *E. tectifica*. *E. dichromophloia* and *E. chlorophylla* had the next lowest values and were not significantly different from each other. The predicted N_{area} values (based on the linear regression) of *E. dichromophloia* increased from 0.96 to 2.01 gN m^{-2} with decreasing rainfall across the distribution of the species. *E. leucophloia*, *E. coolabah*, *E. terminalis*, *E. pruinosa*, and *E. odontocarpa* had similar N_{area} values. The N_{area} values increased with decreasing rainfall from 1.80 to 2.11 gN m^{-2} in the case of *E. leucophloia*, from 1.96 to 2.33 gN m^{-2} in the case of *E. coolabah*, from 1.49 to 2.48 gN m^{-2} in the case of *E. terminalis*, and from 1.89 to 2.50 gN m^{-2} in the case of *E. pruinosa*.

E. gamophylla and *E. pachyphylla* had high N_{area} values that were significantly different from each other and the other species.

The leaf mass per unit area (LMA) of all of the evergreen-tree *Eucalyptus* increased with decreasing rainfall (Figure 4.6). The LMA of the dry-season deciduous *E. confertiflora*, and the three mallee shrubs *E. odontocarpa*, *E. pachyphylla*, and *E. gamophylla* did not vary with decreasing mean annual rainfall.

E. confertiflora had the lowest LMA values of all species (Table 4.1). This was due too there only being very young leaves available for sampling at some of the sites, while fully expanded leaves were sampled on all of the other species. The ranges in the LMA values of the next five species created three groups (in order of increasing mean values); *E miniata* and *E. tectifica*, *E. tetrodonta* and *E. chlorophylla*, and *E. coolabah.* The LMA of *E. miniata* increased from 140.1 to 157.0 g m^{-2} and that of *E. tectifica* increased from 131.6 to 181.8 g m^{-2} with decreasing mean annual rainfall (based on the regression lines). The LMA of *E. tetrodonta* increased from169.0 to 219.3 g m^{-2} and that of *E. chlorophylla* from 163.3 to 228.6 g m^{-2}. The LMA of *E. coolabah* increased from 212.0 to 235.5 g m^{-2} and was significant at $P = 0.06$.

The ranges of the LMA values of the remaining four evergreen trees were not distinguishable. The LMA of *E. dichromophloia* increased from 165.8 to 287.5 g m^{-2}, *E. pruinosa* from 211.5 to 271.5 g m^{-2}, *E. leucophloia* from 224.0 to 273.4 g m^{-2}, and *E. terminalis* from 182.0 to 292.5 g m^{-2} with decreasing rainfall across the distribution of the species (based on the regression lines). The LMA values of *E. gamophylla* were not significantly different from those of *E. terminalis*, while the LMA values of *E. odontocarpa* and *E. pachyphylla* were significantly different from all of the other species and each other.

Since the leaf mass per unit area increased with decreasing mean annual rainfall in the evergreen trees found in the wetter end of the transect (*E. miniata*, *E. tetrodonta*, *E. tectifica*, and *E. chlorophylla*), while the amount of nitrogen per unit area remained unchanged, the amount of nitrogen per unit leaf mass declined with decreasing mean annual rainfall (Figure 4.7). Only *E. dichromophloia* exhibited increases in N_{mass} with decreasing mean annual rainfall. The other eight species showed no trend in N_{mass} with decreasing rainfall. With decreasing mean annual rainfall only one of the 13 species therefore seemed to be increasing the N_{area} values beyond the concentrating effects of the increasing LMA and demonstrating resource substitution.

The N_{mass} values of *E. miniata* were significantly higher than those of *E. tetrodonta*. The predicted values (based on the linear regressions) were between 9.6 and 8.4 mgN g^{-1} in the case of *E. miniata*, and from 7.8 to 6.3 mgN g^{-1} in the case of *E. tetrodonta* as rainfall decreased. *E. tectifica* was sampled in six zones, and the N_{mass} in the northern three zones averaged 10.7 mgN g^{-1} while in the southern three zones it was 6.9 mgN g^{-1}. The change in the predicted N_{mass} values of *E. chlorophylla*, from 10.5 to 7.5 mgN g^{-1} with decreasing rainfall, was predominately the result of two high values at the northernmost site. The increase in N_{mass} with decreasing rainfall found in *E. dichromophloia* was from 6.1 to 7.0 mgN g^{-1}, based on the regression line.

E. confertiflora had N_{mass} values significantly higher than the other *Eucalyptus* species sampled ($\bar{x}$: 10.4 mgN g^{-1}) and had the second highest coefficient of variation after *E. tectifica*. As the canopy was fully dry-season deciduous, when the sampling was done only very young, newly flushed leaves were available on many of the trees. In most of the other species fully expanded leaves were sampled.

The N_{mass} values of *E. pruinosa*, *E. coolabah*, *E. pachyphylla*, and *E. gamophylla* were not significantly different from one another (or from the values of *E. miniata*, *E. tectifica*, and *E. chlorophylla*), and did not change with decreasing rainfall. The remaining three species; *E. leucophloia*, *E. terminalis*, and *E. odontocarpa*, also formed a group without significant differences between their mean N_{mass} values. The N_{mass} values of *E. tetrodonta* and *E. dichromophloia* were significantly lower than all of the other species, but not different from each other.

There was a dilution of N_{mass} with increasing LMA in the evergreen trees at the wetter, northern end of the transect: *E. miniata*, *E. tetrodonta*, *E. tectifica*, and *E. chlorophylla* (Figure 4.8). *E. confertiflora* also exhibited high nitrogen concentrations in the very young, low LMA leaves, so that N_{mass} significantly decreased ($\alpha = 0.05$) with increasing LMA. The pattern of N_{mass} increasing in the leaves of *E. dichromophloia* with decreasing mean annual rainfall was not due to the changes in LMA, as there was no change in N_{mass} with LMA for the species (Figure 4.8i). None of the other species exhibited trends in N_{mass} in relation to changes in LMA.

The changes in LMA were accompanied by a decrease in the leaf carbon concentrations (C_{mass}: mgC g^{-1}) in five of the 13 species which would suggest the increase in LMA was not due to an increase in the lignin content in the leaves (Figure 4.9). C_{mass} increased with increasing LMA in two species, and there was no trend in six species. As the LMA of *E. miniata*, *E. tetrodonta*, *E. chlorophylla* ($P = 0.07$), *E. confertiflora* ($P = 0.08$), and *E. terminalis* increased, the C_{mass} decreased. In *E. dichromophloia* and *E. odontocarpa* ($P = 0.05$) the increase in LMA was accompanied by increases in C_{mass}.

The C_{mass} did not change with decreasing mean annual rainfall in eight of the 13 species (Figure 4.10). C_{mass} decreased with decreasing rainfall in *E. chlorophylla* (from 502.9 to 484.4 mgC g^{-1} based on the values from the linear regression), *E. terminalis* (from 506.5 to 497.3 mgC g^{-1}), and *E. pachyphylla* (from 526.5 to 512.5 mgC g^{-1}), and increased in *E. leucophloia* (from 509.5 to 517.1 mgC g^{-1}) and *E. dichromophloia* (from 495.9 to 516.1 mgC g^{-1}). The C_{mass} values of *E. miniata*, *E. pachyphylla*, and *E. leucophloia* formed a group that were significantly higher (SNK test) than the other species, followed by a group consisting of *E. odontocarpa, E. dichromophloia*, and *E. coolabah*. *E. terminalis* had C_{mass} values significantly different from the other species even though its mean value (500.1 ± 1.0 mgC g^{-1}) placed it at the midpoint of the ranking. The groupings of *E. tetrodonta*, *E. chlorophylla*, and *E. confertiflora* followed by *E. tectifica*, and *E. gamophylla* had overlapping ranges of non-significant differences. *E. pruinosa* had the lower C_{mass} values than all of the other species.

The species mean N_{mass} and C_{mass} values did not depend upon where along the rainfall gradient the species occurred. The species mean LMA, and N_{area} increased as the mean rainfall within the distribution of the species decreased.

4.5 Analysis

In applying the economic analyses developed in Chapter 4.2 to the available data, what was measured (*i.e.* N_{area} at known rainfalls leading to E_T and N_T) are assumed to be the optimal solutions, leaving the dynamics of the cost structures and the importance of resource substitution to be inferred. Given that no gas exchange parameters were measured, the magnitude of the relationships between N_T and A_T, and the total carbon available for resource capture, C_T, are speculative. The dynamics of the responses, resulting from the logic of the analysis, should be more robust demonstrating the relative changes occurring in response to varying resource levels.

If it is assumed that 25% of the incoming rainfall is transpired (Waring & Schlesinger 1985) (with the rest either evaporating from the soil or draining away), then the rainfall gradient (of 200 to 1600 mm yr^{-1}) is from around 2,800 to 22,000 mol {transpired water} m^{-2} {ground area} yr^{-1}. Mean transpiration rates of between 0.0007 and 0.0017 m^3 m^{-2} {leaf area} day^{-1} have been reported for *E. miniata* and *E. tetrodonta* growing near Darwin (O'Grady, Eamus & Hutley 1999), so a value of 0.001 m^3 m^{-2} day^{-1} corresponds to an annual water use of around 20,000 mol m^{-2} {leaf area} yr^{-1}. The stand leaf area index (LAI) would therefore have a predicted value of 1.1 in the wettest areas, which is close to the estimated value of 1.0 (O'Grady et al. 1999).

Without having further data on annual average transpiration values, a simple assumption could be that all of the trees along the transect were using similar amounts of water per unit leaf area as hypothesized by Hatton et al. (1998) for a range of moisture gradients in Australia. Although this pattern has been reported, it would seem logical that in arid areas selection would reduce water-use per unit leaf area, as well as reduce the LAI. Constant water-use per unit leaf area, and the decline in available water, would predict that LAI would therefore have to decrease to 0.14 in the south where mean annual rainfalls were 200 mm yr^{-1} (Figure 4.11a).

The inverse of the LAI measures the ground surface area supporting each unit of leaf area. All of the resources in that unit of leaf area have to be available in that exploitable unit of ground area. The proposed leaf area indices (1.1 to 0.14) translate to an exploitable ground area increasing non-linearly with decreasing rainfall from 0.91 to

7.3 m^2. Just as the water available for transpiration (per unit leaf area) depends on the exploitable ground area and the rainfall per unit ground area, the area-based leaf nitrogen contents depend on the exploitable area and the nitrogen availability per unit ground area. Since the exploitable area is inversely related to rainfall, N_{area} can be expected to be inversely related to rainfall.

The sampled *Eucalyptus* species exhibited a non-linear increase in N_{area} values with decreasing rainfall across the length of the transect. An inverse function;

$$N_{\mathrm{area}} = 0.068 + 33.729/W, \qquad \text{Eq. 4.60}$$

where the mean annual rainfall (W) is in mm yr^{-1}, fitted to the data had an r^2 of 0.52 (Figure 4.11a). A second order polynomial function of N_{area} on rainfall (rather than the inverse) had an r^2 of 0.54, and higher order terms were not significant. The response of N_{area} of the individual species was also predicted from the inverse of mean annual rainfall (Table 4.2; Figure 4.12a). For the individual species the inverse of mean annual rainfall was no better than mean annual rainfall at predicting N_{area}. The variability between trees at the same location masked any potential non-linear trends between locations.

The linear decrease of LAI with rainfall ($LAI = 6.849\mathrm{x}10^{-4}\ W$) meant the N_{T} values decreased linearly with declining rainfall (Figure 4.12b). Where the mesic species were replaced by the more xeric species, between 600 and 800 mm yr^{-1} rainfall, there was a clear difference in the pattern of N_{T} between the two groups, with the xeric species having higher values. *E. dichromophloia*, with its wide distribution spanning both the higher and lower rainfall areas, exhibited N_{T} values reflecting the potential average of the mesic and xeric species.

An instantaneous assimilation rate of 12 μmol m^{-2} s^{-1} and a c_i/c_a of 0.85 (Prior, Eamus & Duff 1997; these data are for saplings, but more recent data of Eamus, Myers, Duff & Williams 1999 on mature trees show similar values for A and A/c_i) was scaled to 67.4 mol m^{-2} yr^{-1} and then used to find the value of f after combining equations 4.46 and 4.48, and assuming $\Gamma = 50$ppm. Vapor pressure deficits were set to 1 kPa across the length of the gradient so the responses to changes in water supply would not be complicated by changes in demand. With E_{T}, N_{T}, and LAI all decreasing with decreasing rainfall, A_{T} inevitably decreased with decreasing rainfall (Figure 4.12c).

At any given point along the transect, increasing either E_T or N_T in isolation would bring decreasing returns in A_T. Both the MP_E (Figure 4.11b) and the MP_N (Figure 4.11c), measuring the response of A_T to potential changes in a single resource, exhibit decreasing rates of return for increasing supply of resources (Equations 4.5, 4.6, and 4.50). Because E_T and N_T covary, the pattern of MP_E and MP_N across the transect differs from the potential response at any point along the transect. MP_E changed little where rainfall was >600 mm yr^{-1}, and MP_N increased across the transect. This could indicate that across the transect water was not limiting, while nitrogen levels were. Increasing levels of N_T brought increasing changes in A_T, while increasing levels of E_T returned decreasing increments in A_T expansion. The partial output elasticities (ε_{AE} and ε_{AN}) measuring the percentage change in A_T with a percentage change in either E_T or N_T show that nitrogen is about 4 times more important than water in determining production levels (Figure 4.11d).

The species at the wetter end of the transect (*E. confertiflora*, *E. miniata*, *E. tectifica*, and *E. tetrodonta*) exhibited sightly increasing or no trends in MP_E values across their distributions (Figure 4.12d). The species at the drier end of the transect had higher MP_E values which decreased with increasing resource levels. The high leaf nitrogen contents of *E. pachyphylla* meant the species was more water limited than any of the others, and therefore had high MP_E values. The patterns of the species MP_N values were opposite the patterns of the MP_E values (Figure 4.12e). The species from areas with rainfalls less than around 800 mm yr^{-1} had increasing rates of return per unit nitrogen invested, while those from the wetter areas had decreasing or constant rates of return per unit nitrogen invested. The MP_N values of the mesic species were higher than the xeric species indicating that they were more N limited than the species from the drier areas. The patterns of the partial output elasticities of the individual species (Figures 4.12f and 4.12g) follow those of the MP_E and MP_N values. In the wetter areas the species are around 4 times more responsive to changes in N_T than E_T, but the elasticities are relatively constant across the ranges of the species. In the drier areas the species show decreasing sensitivity to increasing water supply levels and increasing sensitivity to increasing N supply levels.

The potential ability to substitute nitrogen for water without changing the overall productivity, i.e. the $MRTS_{N,E}$, was higher in the wetter areas and decreased with decreasing mean annual rainfall (Figure 4.11e). The inverse ($MRTS_{E,N}$) therefore increased with decreasing rainfall. The $MRTS_{N,E}$ values of the mesic species were higher than those of the xeric species, and *E. dichromophloia*, with a distribution spanning both groups, had values that made a transition between the two groups (Figure 4.12g). The elasticity of substitution of the model (ε_{EN} or ε_{NE}; Equation 4.42) is a constant ½ regardless of resource levels.

Enumerating the cost function (Equation 4.2) without any data requires some arbitrary decisions. The calculated N_T probably included a considerable quantity of recycled N, and therefore overestimates an annual N uptake rate. A better way of costing the canopy N content would be by measuring the N lost in litterfall. The carbon cost of resource uptake also needs to be measured as carbon lost in fine root turnover and respiration, rather than as total root mass which would primarily consist of semi-permanent structures. One mole of carbon per m^2 of available area (the inverse of LAI) per resource was arbitrarily chosen as the investment required to yield the calculated E_T and N_T values. This represents about 75% of A_T at the dry end of the transect and 2.5% of A_T at the wet end of the transect (Figure 4.11f). With C_T defined, the solutions for the relative values of C_E and C_N can be found (Figure 4.11g). The carbon cost of water increases dramatically as rainfall drops below 400 mm yr^{-1}, and over the transect increases around 130-fold while the cost of nitrogen increases about 19-fold.

Since the carbon costs of resource uptake per unit ground area were assumed to be similar for all of the species, the variation in total cost of resource uptake was dependent only on the variation in the ground area being exploited. The uptake efficiency (the inverse of the total carbon cost per unit resource returned) varied as resource levels varied. Those species with high N_T are therefore predicted to be able to attain these values due to high uptake efficiencies, or low carbon costs per unit return (Figure 4.12k). *E. pachyphylla*, with high N_T values, therefore has low C_N values. Because all species have the same E_T, the differences in the C_E values between co-occurring species was due to the patterns in C_N (Figure 4.12j). *E. pachyphylla*, which had low expenditure of carbon per unit gain in canopy N, therefore has more carbon to invest for a constant water return which was reflected in a high C_E.

The change in water use with the change in the cost of water across the transect consisted of two components: the substitution effect, and the income effect (Figure

4.11h). All across the transect there was a decrease in water use with increasing cost reflected by the negative values of $\partial E_{\mathrm{T}}^{*} / \partial C_{\mathrm{E}}$. The highest values occurred at the wetter end of the transect where the costs of water were low (Figure 4.11i). The differences in the change in water use with the change in cost, the substitution effect, and the income effect ($\partial E_{\mathrm{T}}^{*} / \partial C_{\mathrm{E}}$, *SE*, and *IE*) between the species were subtle since they arise from the differences in the cost of nitrogen between the species (Figures 4.12l, 4.12m, and 4.12n). When *SE* is expressed as a fraction of $\partial E_{\mathrm{T}}^{*} / \partial C_{\mathrm{E}}$ (Figure 4.13) it becomes clearer that in the mesic species around 70% of the change in water use is due to substituting nitrogen for water, while the remaining 30% of the change in water use is due to the change in the cost of water. In the xeric species 55 to 60% of the change in water use is due to resource substitution and the remainder is due to changes in resource availability.

Since both water and nitrogen use increase with increasing allocation to resource acquisition, they can both be considered as "normal goods" based on the signs of the solutions of Equations 4.43 and 4.44. Increasing use of either resource enhances the marginal product of the other, so they can be described as cooperative factors of production as determined by the sign of the solution of Equation 4.34. The behaviors of all of the individual species follow the patterns of the general community on these two issues.

4.6 Discussion

The theoretical analyses developed by economists have obvious applications to ecophysiology (Bloom et al. 1985; Gleeson & Tilman 1992; Lerdau 1992). That organisms would evolve toward the optimal solution determining growth under the constraints of multiple resource limitations is the only self-evident law in the field of ecology. Attempting to find specific examples of organisms optimally suited to specific suits of environmental constraints is, however, a mis-application of a law that should only be stated in probability density functions or as the patterns of the central tendencies of large data sets.

The Northern Territory is a good place to examine optimization of ecophysiological process since it has probably had a stable climate for a long period of time (Pole & Bowman 1996). The topography is not complex, and although the area has been grazed and burns regularly, the overstory is relatively undisturbed. Broadly, the wetter northern areas, as with most of the coastal areas of Australia, is dominated by Eucalypts, while the arid southern area, as with the rest of central Australia, is dominated by N-fixing Acacias. The success of the growth strategy emphasizing high investments for N acquisition in the drier areas would seem to be an example of resource substitution.

The importance of N as a greater limit on productivity than water supply was emphasized by the partial output elasticity of N which was around 4 times higher than that of water across the transect. The highly seasonal rainfall, especially in the area north of 16°S that is dominated by the monsoon (Cook & Heergeden 1997; Heerdegen & Cook 1999), may result in little water limitation over much of the transect, for half of the year. During the other half of the year all the trees along the transect are equally dependant on soil water storage. The increase in the marginal product of nitrogen towards the wetter northern regions also emphasizes the importance of N limitation as water becomes less limiting.

Increasing only one resource in isolation yields diminishing returns, reflected in the fact that at any point along the transect the slopes of the marginal products of both N and water are negative. The actual pattern of resource availability across the transect, where there are increasing levels of both N and water in the overstory canopy towards the north, results in increasing marginal products of N. The increase in water use could be interpreted as being higher than optimal as there are decreasing values for its marginal product. The amount of water to be substituted for N was highest in the drier southern areas where there were high area-based leaf N contents, and then decreased towards the north with increasing water use. The structure of the simple model developed found water and nitrogen to be equally substitutable, and independent of environmental conditions, since the elasticity of substitution was a constant 0.5 for each resource. This would probably not be the case if assimilation was described by a saturating function of c_i, and both A_T and E_T were dependent on leaf temperatures.

Economics has a well developed mathematical treatment of optimal resource use, and cost minimizing investment strategies developed from the calculus of variations. The mathematics involved in finding the optimal levels of resource use of a constrained production function can be inverted to explore the underlaying cost structure from an observed pattern of resource use. The scarcity of N was reflected in its cost of uptake being between 5 and 6 orders of magnitude higher than water per mole in the canopy. Even if 90% of the current canopy N content was recycled it would only decrease the relative cost of N uptake compared to water by one order of magnitude.

Simply relating the required root investment to the available ground area probably underestimates investment in the wetter area where individuals are closer together and clearly competing for resources. Under such conditions higher investments of carbon in root growth would increase the probability of being the closest root to a newly released resource. Without considering these biotic factors, the costs of resource uptake increased the most in the driest 1/3 of the transect.

The change in the optimal rate of water use, as the cost of water varies across the transect, reflects both the change in the amount of carbon available to invest toward its uptake, and the substitution of N for water. The ‘substitution effect’ component of the Slutsky equation directly measures the role of increased N usage toward water conservation. At the wetter end of the transect, where N usage was low, the increasing N in the canopy as rainfall decreased was responsible for around 70% of the changes in the optimal rate of water use. The effectiveness of resource substitution decreased to around 40% at the highest total canopy N contents in the driest areas.

In the northern areas, the decrease in water use due to resource substitution with decreasing water availability was not due to measurable increases in N_{area}, but rather due to the maintenance of N_{area} with increasing costs. In the drier areas there were clear increases in N_{area} with decreasing water availability.

The N_{area} contents decreased with decreasing mean annual rainfall across the sampled distributions of all of the evergreen-tree species growing in the southern, drier part of the transect (*E. pruinosa*, *E. coolabah*, *E. leucophloia*, *E. dichromophloia*, and *E. terminalis*). In contrast to these five species, the three mallee shrubs (*E. odontocarpa*, *E. pachyphylla*, and *E. gamophylla*) also found in the driest areas did not exhibit changes in N_{area} across their distributions in response to decreasing mean annual rainfall. The single completely drought deciduous species that was sampled (*E. confertiflora*), and the four evergreen species occurring in the wetter, northern part of the transect (*E. miniata*, *E tetrodonta*, *E. tectifica*, and *E. chlorophylla*) showed no changes in N_{area} across their distributions with decreasing rainfall. There was a significant correlation between the species mean N_{area} value and the mean rainfall occurring within the distribution of the species. The species with low N_{area} values in the high rainfall regions were replaced by species with high N_{area} values in the drier regions. The leaf N values found in this study are similar to those reported for Eucalypts and other over story species at a similar set of sites across the Northern Territory of Australia (Schulze et al. 1998), at a site near Darwin (Eamus et al. 1999), and *Eucalyptus* species growing in other parts of Australia (Mooney et al. 1978).

The zone-mean LMA values (of all the species sampled within a zone) doubled across the decreasing rainfall gradient, and increased in all of the evergreen tree species, emphasizing the increased investment in leaf carbon required to withstand water stress. The LMA did not change across the distribution of the dry-season fully deciduous species, nor across the distributions of the three multi-stemmed mallee shrub species. The increasing LMA in the four evergreen species in the wetter part of the transect, while their N_{area} values were unchanged, meant these species exhibited decreasing N_{mass} values with decreasing rainfall. All of the other species exhibited constant N_{mass} values with decreasing rainfall, except *E. dichromophloia* which exhibited increasing values. The patterns of increasing N_{area}, and presumably increasing assimilation capacities, with decreasing rainfall in the evergreen tree species in the drier half of the transect would reduce the payback period for these increasingly expensive leaves.

Varying responses of N_{area} and LMA to decreasing rainfall have been reported for co-occurring closely related species in the Mediterranean-type ecosystems of Spain (Castro-Diez et al. 1997). They found a deciduous *Quercus* species and one of the two evergreen species exhibited no response to decreasing rainfall while the other evergreen species studied show increasing N_{area} and LMA with increasing rainfall. LMA significantly increased with increasing rainfall in one of the evergreen species, and the mass-based lignin concentrations increased with increasing rainfall in both evergreen species, but neither LMA nor lignin concentration responded in the deciduous species.

In a single species studied along a rainfall gradient in Argentina, Buamscha et al. (1998) found the highest concentrations of mass-based leaf nitrogen occurred at the driest site, followed by the wettest site, while the intermediate sites had the lowest values. The lignin contents of the leaves at the driest site were also lower than at the other sites. As leaves matured the mass-based leaf carbon concentration decreased.

Changes in LMA can result from either changes in leaf thickness or changes in leaf density, or changes in both. Although it has been reported that the changes in LMA are not usually the result of simultaneous changes in both thickness and density (Wilson, Thompson & Hodgson 1999), both have been shown to respond to manipulations of nutrients, moisture, and light and these factors need to be accounted for in order to fully explain changes in LMA (Witkowski & Lamont 1991).

Unlike the patterns of N_{area} with decreasing rainfall, which depended on both growth form and location, the patterns of LMA with decreasing rainfall were only dependent on growth form. All of the evergreen species responded to decreasing mean available rainfalls with increasing LMA. LMA would be expected to increase with decreasing rainfall, and the lack of a trend in the deciduous species is consistent with the expected response of a species avoiding drought rather than tolerating it. The mallee shrubs were again highly variable, possibly masking trends, or were unable to exhibit significant plasticity.

There was an increase in C_{mass} with increasing LMA in only two of the species (only one significant at 0.05), so changes in LMA are unlikely to has arisen from increases in C rich compounds such as lignin. The mass-based leaf carbon contents decreased with increasing LMA in five species (three significantly at 0.05) where the shift in leaf chemistry was towards compounds containing lower C (and less N) in the tissues.

The increase in N_{area} with decreasing rainfall has provoked some confusion (Dijkstra 1989) and been attributed to the increased light levels in the more open canopies found in drier areas (Mooney et al. 1978; Cunningham et al. 1999). As the leaves in this study were all collected from the upper, sun-exposed parts of the canopy, the patterns of increasing N_{area} with decreasing mean annual rainfall are probably not due to light gradients as found within canopies causing gradients of N (Field 1983; Evans 1989). As the overstory tree leaf area decreases with decreasing rainfall, the understory species may receive higher light levels and respond with higher leaf N concentrations, but this study concentrated on the responses of the leaves at the top of the overstory canopy. Because nitrogen is a substitutable resource when water availability decreases, the pattern of increasing N_{area} with decreasing rainfall does not require the interaction of another environmental variable to explain the expected and observed pattern.

Instead, what must be explained is why the pattern was not completely universal and occurring in all species. From the modeling exercises of Buckley et al. (2002), for the N_{area} in the top layers of the canopy to remain constant, as was found in the evergreen species in the north, the ratio of N_t and E_t needs to be maintained. As rainfall decreases from 1600 to 800 mm yr^{-1} there needs to be an equivalent decrease in available N. Nitrogen availability then needs to remain constant across the southern ½ of the transect while rainfall continues to decrease. The alternative is that the rainfall gradient may not reflect the gradient in water availability. The monsoonal climate, where 80% of the annual rainfall occurs in 4 - 5 months would seem a more logical explanation. At rainfalls greater than ~800 mm yr^{-1} the increasing rainfall only contributes to overland flow and there is not necessarily an increase in available water during the growth season for trees. These areas may also retain available water within the rooting zone, so that even during the dry season there is not a strong gradient in water availability (Williams et al. 1997). Canopy water flux measurements near Darwin show transpiration rates continue at high levels all during the dry season (O'Grady et al. 1999; Eamus, O'Grady & Hutley 2000; Hutley, O'Grady & Eamus 2000). Carbon isotope measurements reveal little change between rainfalls of 1600 to 400 mm yr^{-1} (Schulze et al. 1998; Miller et al. 2001).

The single drought deciduous species did not exhibit the pattern of increasing N_{area} with decreasing rainfall. This would indicate that the species was also probably not experiencing a gradient in water availability. Instead of responding to increasing aridity with physiological adjustments, the species probably just retains its canopy for decreasing time periods while there is sufficient soil moisture.

The lack of the pattern in the 3 mallee shrubs could either be due to the narrow rainfall range over which the species occurred and the variability in N_{area} values obscuring trends, or it could be that the growth form has significantly different rooting patterns from the co-occurring trees and can not gain a greater return for an increased investment in N_{area}. The mallee shrubs may also not be able to exhibit significant plasticity in either morphology or physiology, which would be a conservative strategy suitable for extreme environments and would also explain their relatively narrow distributional ranges.

Although the display of N_{area} is conceptually independent from that of C_{area}, and responding to independent selection pressures, within a species N_{area} and C_{area} may be allometrically linked. A species may have a genetic program to maintain leaf cells of a certain C:N ratio, and plasticity in varying the number of cells in leaf thickness or the amount of air space around the cells. Changing cell size would probably affect the C:N ratio as walls are mainly C and the cell volume related to N content (Roderick, Berry & Noble 1999).

Leaf mass per unit area, or the inverse of LMA; specific leaf area, is often thought to be a more easily measured functional substitute for N_{area} (Westoby 1998). Leaf dry matter (Wilson et al. 1999), or leaf water content (Roderick et al. 1999) have also been proposed to be better parameters than SLA for expressing the functioning of leaves. However, across this transect the LMA values did not consistently reflect the patterns of N_{area}.

Leaf nitrogen concentrations (N_{mass}) were diluted by the increasing LMA in *E. miniata*, *E tetrodonta*, *E. tectifica*, and *E. chlorophylla*, while the other species maintained N_{mass} values as LMA increased. In *E. confertiflora* the extremely young leaves had high N_{mass} values as the nitrogen seems to be allocated before the carbon is available to expand the leaves. Only *E. dichromophloia* and *E. odontocarpa* exhibited increasing leaf carbon contents (C_{mass}) with increasing LMA, possibly indicating an increasing proportion of lignin in the leaves. *E. miniata*, *E. tetrodonta*, *E. chlorophylla*, *E. confertiflora*, and *E. terminalis* all showed decreasing C_{mass} with increasing LMA. Schmidt & Stewart (1998) have found that nitrogen can be stored in bark during the wet season.

Although the responses of N_{area} and N_{mass} to decreasing mean annual rainfall were similar within the evergreen species at the wet end of the transect, and within the evergreen species at the dry end of the transect, the lack of a single common pattern (Field 1991) demonstrates that simple generalizations of plant responses to stress are not possible. The idea that all environmental stresses manifest themselves in a single physiological response (Chapin 1991) was not observed. Decreasing water availability brought on consistent changes in some morphological characteristics (LMA), but divergent responses in other characteristics (N_{area}), and depended on growth form and environmental conditions.

The diversity of patterns in N_{area} with decreasing mean annual rainfall reflected differences in the costs of acquiring N and water along the transect. The wetter areas where N_{area} did not change with decreasing water availability had higher rates of water savings due to resource substitution than in the drier areas where N_{area} increased with decreasing rainfall. The importance of resource substitution as a dynamic response to the changing costs of acquiring resources resulting from changes in their availability is therefore not always easily apparent. The economic analyses that describe the phenomena seem to imply that it is important and would maximize returns when there is a limited ability to invest for resource uptake.

4.7 Literature Cited

Andersen, A.N., Braithwaite, R.W., Cook, G.D., Corbett, L.K., Williams, R.J., Douglas, M.M., Gill, A.M., Setterfield, S.A. & Muller, W.J. (1998) Fire research for conservation management in tropical savannas: Introducing the Kapalga fire experiment. Australian Journal of Ecology 23, 95-110.

Bloom, A.J., Chapin, F.S., III & Mooney, H.A. (1985) Resource limitation in plants - an economic analogy. Ann Rev Ecol Syst 16, 363-392.

Brooker, M.I.H. & Kleinig, D.A. (1994) Field Guide to Eucalypts: Volume 3 Northern Australia. Inkata Press, Sydney.

Buamscha, G., Gobbi, M., Mazzarino, M.J. & Laos, F. (1998) Indicators of nitrogen conservation in *Austrocedrus chilensis* forests along a moisture gradient in Argentina. Forest Ecology and Management 112, 253-261.

Buckley, T.N., Miller, J.M. & Farquhar, G.D. (2002) The mathematics of linked optimisation for water and nitrogen use in a canopy. Silva Fennica 36, 639-669.

Castro-Diez, P., Villar-Salvador, P., Perez-Rontome, C., Maestro-Martinez, M. & Monserrat-Marti, G. (1997) Leaf morphology and leaf chemical composition in three *Quercus (Fagaceae)* species along a rainfall graidnet in NE Spain. Trees 127-134.

Chapin, F.S., III (1991) Integrated responses of plants to stress. BioScience 41, 29-36.

Cook, G. & Heergeden, R. (1997) The length of the rainy season can be more important than the amount of rain for savannas in the Northern Territory. Australian Collaborative Land Evaluation Program Newsletter 6, 18-20.

Cunningham, S.A., Summerhayes, B. & Westoby, M. (1999) Evolutionary divergences in leaf structure and chemistry, comparing rainfall and soil nutrient gradients. Ecological Monographs 69, 569-588.

Dawson, T.E. & Pate, J.S. (1996) Seasonal water uptake and movement in root systems of Australian phraeatophytic plants of dimorphic root morphology: a stable isotope investigation. Oecologia 107, 13-20.

Dijkstra, P. (1989) Cause and effect of differences in specific leaf area. In: Causes and consequences of variation in growth rate and productivity of higher plants (H. Lambers, M. L. Cambridge, H. Konings and T. L. Pons), 125-140. SPB Academic Publishing, The Hague.

Eamus, D., Myers, B., Duff, G. & Williams, R. (1999) A cost-benefit analysis of leaves of eight Australian savanna tree species of differing leaf life-span. Photosynthetica 36, 575-586.

Eamus, D., Myers, B., Duff, G. & Williams, R. (1999) Seasonal changes in photosynthesis of eight savanna tree species. Tree Physiology 19, 665-671.

Eamus, D., O'Grady, A.P. & Hutley, L. (2000) Dry season conditions determine wet season water use in the wet-dry tropical savannas of northern Australia. Tree Physiology 20, 1219-1226.

Evans, J.R. (1989) Partitioning of nitrogen between and within leaves grown under different irradiances. Aust. J. Plant Physiol. 16, 533-548.

Evans, J.R. (1989) Photosynthesis and nitrogen relationships in leaves of C_3 plants. Oecologia 78, 9-19.

Farquhar, G.D., Buckley, T.N. & Miller, J.M. (2002) Optimal stomatal control in relation to leaf area and nitrogen content. Silva Fennica 36, 625-637.

Field, C. (1983) Allocating leaf nitrogen for the maximization of carbon gain: leaf age as a control on the allocation program. Oecologia 56, 341-347.

Field, C., Merino, J. & Mooney, H.A. (1983) Compromises between water-use efficiency and nitorgen-use efficiency in five species of California evergreens. Oceologia 60, 384-389.

Field, C.B. (1991) Ecological scaling of carbon gain to stress and resource availability. In: Response of Plants to Multiple Stresses (H. A. Mooney, W. E. Winner and E. J. Pell), 35-65. Academic Press, San Diego.

Gleeson, S.K. & Tilman, D. (1992) Plant allocation and the multiple limitation hypothesis. The American Naturalist 139, 1322-1343.

Grime, J.P. (1979) Plant Strategies and Vegetation Processes. John Wiley & Sons, New York.

Harvey, P.H. & Pagel, M.D. (1991) The comparative method in evolutionary biology. Oxford University Press, Oxford.

Hatton, T., Reece, P., Taylor, P. & McEwan, K. (1998) Does leaf water efficiency vary among eucalypts in water-limited environments? Tree Physiology 18, 529-536.

Heerdegen, R.G. & Cook, G.D. (1999) Redefining wetness by dryness: The duration and extent of the north Australian monsoon. In: Proceedings, 20th New Zealand Geography Conference (M. Roche, M. McKenna and P. Hesp), 139-143. New Zealand Geographical Society, Hamilton N.Z.

Hutley, L.B., O'Grady, A.P. & Eamus, D. (2000) Evapotranspiration from Eucalypt open-forest savanna of Northern Australia. Functional Ecology 14, 183-194.

Lerdau, M. (1992) Future discounts and resource allocation in plants. Functional Ecology 6, 371-375.

Miller, J.M., Williams, R.J. & Farquhar, G.D. (2001) Carbon isotope discrimination by a sequence of *Eucalyptus* species along a subcontinental rainfall gradient in Australia. Functional Ecology 15, 222-232.

Mooney, H.A., Ferrar, P.J. & Slatyer, R.O. (1978) Photosynthetic capacity and carbon allocation patterns in diverse growth forms of *Eucalyptus*. Oecologia 36, 103-111.

Mooney, H.A. & Gulmon, S.L. (1979) Environmental and evolutionary constraints on the photosynthetic characteristics of higher plants. In: Topics in plant population biology (O. T. Solbrig, S. Jain, G. B. Johnson and P. H. Raven), 316-337. Columbia University Press, New York.

Mooney, H.A. & Gulmon, S.L. (1982) Constraints on leaf structure and function in relation to herbivory. BioScience 32, 198-206.

O'Grady, A.P., Eamus, D. & Hutley, L.B. (1999) Transpiration increases during the dry season: patterns of tree water use in eucalypt open-forests of northern Australia. Tree Physiology 19, 591-597.

Pate, J.S., Jeschke, W.D. & Aylward, M.J. (1995) Hydraulic architecture and xylem structure of the dimorphic root systems of South-West Australian species of Proteaceae. Journal of Experimental Botany 46, 907-915.

Pole, M.S. & Bowman, D.M.J.S. (1996) Tertiary plant fossils from Australia's 'Top End'. Australian Systematic Botany 9, 113-126.

Prior, L.D., Eamus, D. & Duff, G.A. (1997) Seasonal and diurnal patterns of carbon assimilation, stomatal conductance and leaf water potential in *Eucalyptus tetrodonta* saplings in a wet-dry savanna in northern Australia. Australian Journal of Botany 45, 241-258.

Roderick, M.L., Berry, S.L. & Noble, I.R. (1999) On the relationship between leaf composition and morphoogy at elevated CO_2. New Phytologist 143, 63-72.

Schulze, E.-D., Williams, R.J., Farquhar, G.D., Schulze, W., Langridge, J., Miller, J.M. & Walker, B.H. (1998) Carbon and nitrogen isotope discrimination and nitrogen nutrition of trees along a rainfall gradient in northern Australia. Australian Journal of Plant Physiology 25, 413-425.

Stewart, G.R., Turnbull, M.H., Schmidt, S. & Erskine, P.D. (1995) ^{13}C natural abundance in plant communities along a rainfall gradient: a biological integrator of water availability. Australian Journal of Plant Physiology 22, 51-55.

Thompson, A.A., Jr. & Formby, J.P. (1993) Economics of the firm. Prentice Hall, New Jersey.

Toumanoff, P. & Nourzad, F. (1994) A mathematical approach to economic analysis. West Publishing, New York.

Waring, R.H. & Schlesinger, W.H. (1985) Forest Ecosystems: Concepts and Management. Academic Press, New York.

Westoby, M. (1998) A leaf-height-seed (LHS) plant ecology strategy scheme. Plant and Soil 199, 213-227.

Williams, R.J., Myers, B.A., Muller, W.J., Duff, G.A. & Eamus, D. (1997) Leaf phenology of woody species in a north Australian topical savanna. Ecology 78, 2542-2558.

Wilson, P.J., Thompson, K. & Hodgson, J.G. (1999) Specific leaf area and leaf dry matter content as alternative predictors of plant strategies. New Phytologist 143, 155-162.

Witkowski, E.T.F. & Lamont, B.B. (1991) Leaf specific mass confounds leaf density and thickness. Oecologia 88, 486-493.

4.8 Tables and Figures

Table 4.1 Mean (±SE) mean annual rainfall with in the sampled distribution of the species, N_{area}, and LMA. The ranges of non-significant differences (SNK test) are given by the superscripts.

Species	Mean annual rainfall (mm)	Species	N_{area} (gN m^{-2})	Species	LMA (g m^{-2})
E. miniata	1157 ± 37^{a}	*E. confertiflora*	1.18 ± 0.03^{a}	*E. confertiflora*	116.0 ± 2.9^{a}
E. tetrodonta	1123 ± 41^{a}	*E. miniata*	1.32 ± 0.03^{a}	*E. miniata*	148.8 ± 2.4^{b}
E. tectifica	1081 ± 34^{a}	*E. tetrodonta*	1.35 ± 0.02^{a}	*E. tectifica*	160.2 ± 4.8^{b}
E. confertiflora	852 ± 25^{b}	*E. tectifica*	1.38 ± 0.06^{a}	*E. tetrodonta*	196.8 ± 3.8^{c}
E. chlorophylla	776 ± 11^{bc}	*E. dichromophloia*	1.60 ± 0.05^{b}	*E. chlorophylla*	198.1 ± 7.4^{c}
E. dichromophloia	708 ± 28^{c}	*E. chlorophylla*	1.73 ± 0.07^{b}	*E. coolabah*	223.9 ± 4.7^{d}
E. coolabah	557 ± 20^{d}	*E. leucophloia*	1.99 ± 0.05^{c}	*E. dichromophloia*	240.3 ± 5.3^{e}
E. pruinosa	522 ± 19^{d}	*E. coolabah*	2.15 ± 0.06^{cd}	*E. pruinosa*	248.6 ± 4.1^{e}
E. leucophloia	479 ± 22^{d}	*E. terminalis*	2.18 ± 0.05^{cd}	*E. leucophloia*	253.8 ± 3.8^{e}
E. terminalis	352 ± 8^{e}	*E. pruinosa*	2.27 ± 0.05^{d}	*E. terminalis*	259.0 ± 4.2^{ef}
E. odontocarpa	386 ± 14^{ef}	*E. odontocarpa*	2.27 ± 0.07^{d}	*E. gamophylla*	273.6 ± 5.6^{f}
E. pachyphylla	306 ± 6^{ef}	*E. gamophylla*	2.52 ± 0.10^{e}	*E. odontocarpa*	293.5 ± 7.2^{g}
E. gamophylla	253 ± 6^{f}	*E. pachyphylla*	3.39 ± 0.11^{f}	*E. pachyphylla*	384.8 ± 8.2^{h}

Table 4.2 The relationships between area-based leaf nitrogen contents (N_a; mol m^{-2}) and rainfall (W; mm yr^{-1})used in the econometric analyses in Chapter 4.5.

Species	N_a
E. chlorophylla	$0.094 + 22.970/W$
E. confertiflora	$0.091 - 6.040/W$
E. coolabah	$0.112 + 21.748/W$
E. dichromophloia	$0.053 + 37.715/W$
E. gamophylla	$0.142 + 9.330/W$
E. leucophloia	$0.115 + 11.772/W$
E. miniata	$0.093 - 4.257/W$
E. odontocarpa	$0.126 + 12.681/W$
E. pachyphylla	$0.230 + 3.575/W$
E. pruinosa	$0.109 + 25.350/W$
E. tectifica	$0.138 - 41.688/W$
E. terminalis	$0.084 + 24.632/W$
E. tetrodonta	$0.093 + 3.635/W$

Figure Legends

Figure 4.1

The total canopy assimilation predicted by the simple model developed as a function of the total canopy transpiration and total canopy leaf nitrogen content. The contour intervals (isoquants) on the surface reflect $\{E_T, N_T\}$ combinations that yield a constant total assimilation, A_{T*}.

Figure 4.2

The relationship between the isoquant, the isocost line, and the optimal ratio of E_T and N_T.

Figure 4.3

Analysis of the change in the optimal ratio of resource use with a decrease in rainfall from 800 to 400 mm/yr. The observed ratio of E_T and N_T at a rainfall of 800 mm/yr reflects point *A* which is the tangent of an isoquant and isocost line. At 400 mm/yr rainfall the observed ratio of E_T and N_T is at point *C*. Had there not been a shift in the ratio of consumed resources, the same total assimilation would have required resources denoted at point *B* which has a higher total cost. The change in resource use from point *A* to point *B* reflects the income effect, while the change from point *B* to point *C* reflects the substitution effect.

Figure 4.4

a) The predicted mean annual rainfall and wet season (December to March) rainfall (ANUCLIM 1.8, Centre for Resource and Environmental Studies, ANU) in the 33 zones where samples were collected.

b) The locations where samples where collected along the transect. The open circles denote zones where the species could not be found and was skipped over. The spacing between samples varies because not all species within a zone were sampled at exactly the same location.

Figure 4.5

The leaf nitrogen content per unit area (N_{area}: gN m^{-2}) in relation to the predicted mean annual rainfall across the distributions of the 13 sampled species. Ten leaves were combined to make the one sample per tree. The regression lines are shown where the trend with mean annual rainfall was significant ($\alpha = 0.05$).

Figure 4.6

The leaf mass per unit area (LMA: g leaf m^{-2}) in relation to the predicted mean annual rainfalls across the distributions of the 13 sampled species. The trend for *E. coolabah* was significant at $P = 0.06$.

Figure 4.7

The leaf nitrogen concentrations on a mass-basis (N_{mass}: mgN g^{-1} leaf) in relation to the predicted mean annual rainfalls across the distributions of the 13 sampled species.

Figure 4.8

The response of N_{mass} to increasing LMA in the 13 sampled species.

Figure 4.9

The response of leaf carbon content per unit mass (C_{mass}: mgC g^{-1}) to increasing LMA in the 13 sampled species.

Figure 4.10

The C_{mass} in relation to the predicted mean annual rainfalls across the distributions of the 13 sampled species.

Figure 4.11

The various econometric parameters calculated for all of the sampled overstory *Eucalyptus* species combined:

a) The area-based leaf nitrogen content (N_a) was calculated from Equation 4.60, and the leaf area index (*LAI*)from the mean annual rainfall and assumptions including that there were similar transpiration rates per unit leaf area for all species at all locations across the rainfall gradient, allowing the total canopy nitrogen content to be calculated (N_T).

b+c) The marginal products of water and nitrogen when moving across the rainfall gradient (solid lines) and at selected locations with hypothetical changes in a single resource (dashed lines). The actual water and nitrogen supply co-vary across the gradient, while at specific locations it is possible to predict the response to increases of a single resource in isolation.

d) The partial output elasticities of total canopy assimilation to changes in either water or nitrogen supply allowing the relative sensitivities to the two resources to be directly compared across the rainfall gradient.

e) The marginal rates of technical substitution (i.e. the rate at which one resource can be substituted for the other yielding the same total canopy assimilation) across the rainfall gradient. $MRTS_{NE}$ is the rate at which nitrogen can be substituted for water, and $MRTS_{EN}$ is the inverse (the rate which water can be substituted for nitrogen).

f) The predicted total canopy assimilation (A_T; top line), the total cost of resource uptake (C_T; second line), and the cost of nitrogen (cost per unit and amount C_N*N_T; third line) and water (C_E*E_T; bottom line).

g) The carbon cost (mol mol^{-1}) of water (C_E) and nitrogen (C_N) across the rainfall gradient.

h) The change in water use with the change in the cost of water across the rainfall gradient ($\partial E_T/\partial C_E$; bottom line), and its two components; the substitution effect (*SE*; middle line), and the income effect (*IE*; top line).

i) The change in water use with the change in the cost of water ($\partial E_T/\partial C_E$; bottom line), and its two components; the substitution effect (*SE*; middle line), and the income effect (*IE*; top line) in relation to the range of the cost of water calculated to occur across the rainfall gradient.

Figure 4.12

The various econometric parameters calculated for each of the *Eucalyptus* species separately in relation to the mean annual rainfall occurring across the distribution of each of the species:

a) The regression lines describing the observed area-based leaf nitrogen contents (N_a; mol m^{-2}{leaf}) from Table 4.2.

b) The calculated total canopy nitrogen contents (N_T; mol m^{-2}{ground}) for each of the species.

c) The calculated total canopy assimilation rate (A_T; mol m^{-2}{ground}) for each of the species (Equation 4.50).

d) The marginal product of water for each of the species (from Equation 4.5).

e) The marginal product of nitrogen for each of the species (from Equation 4.6).

f) The elasticity of demand for water for each of the species (from Equation 4.7).

g) The elasticity of demand for nitrogen for each of the species (from Equation 4.8).

h) The marginal rate of technical substitution of water for nitrogen (from Equation 4.10).

i) The marginal rate of technical substitution of nitrogen for water (from Equation 4.11).

j) The carbon cost of water (from Equation4.55).

k) The carbon cost of nitrogen (from Equation4.56).

l) The change in water-use with the change in the cost of water (from Equation 4.59)

m) The substitution effect part of the change in water-use with the change in the cost of water.

n) The income effect part of the change in water-use with the change in the cost of water.

Figure 4.13

The substitution effect as a fraction of the change in water-use with changing cost of water across the transect.

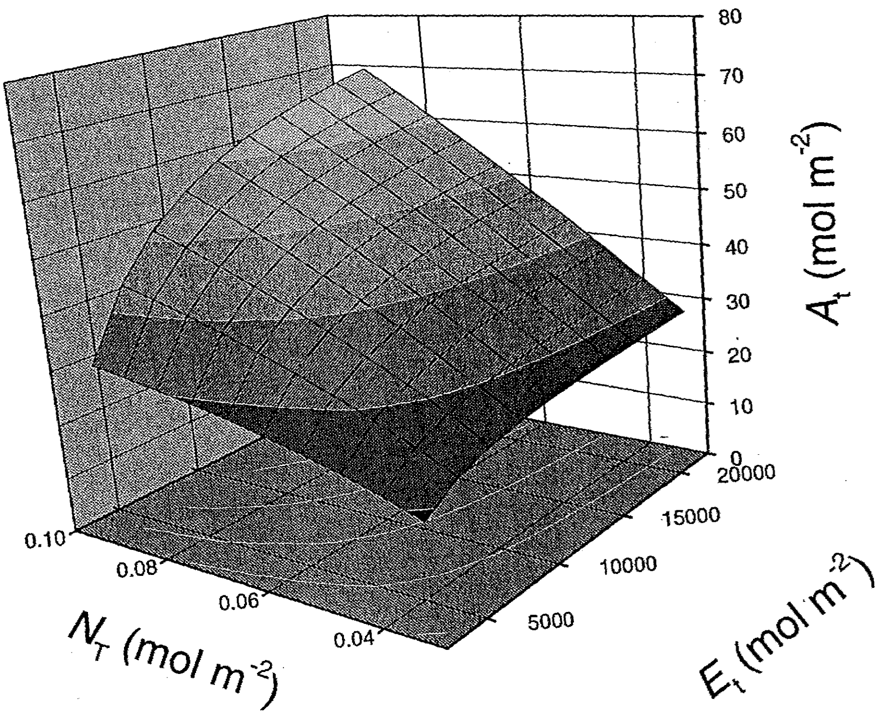

80
70
60
50
40
30
20
10
0
A_t (mol m^{-2})
20000
15000
10000
5000
E_t (mol m^{-2})
0.10
0.08
0.06
0.04
N_T (mol m^{-2})

Figure 4.1

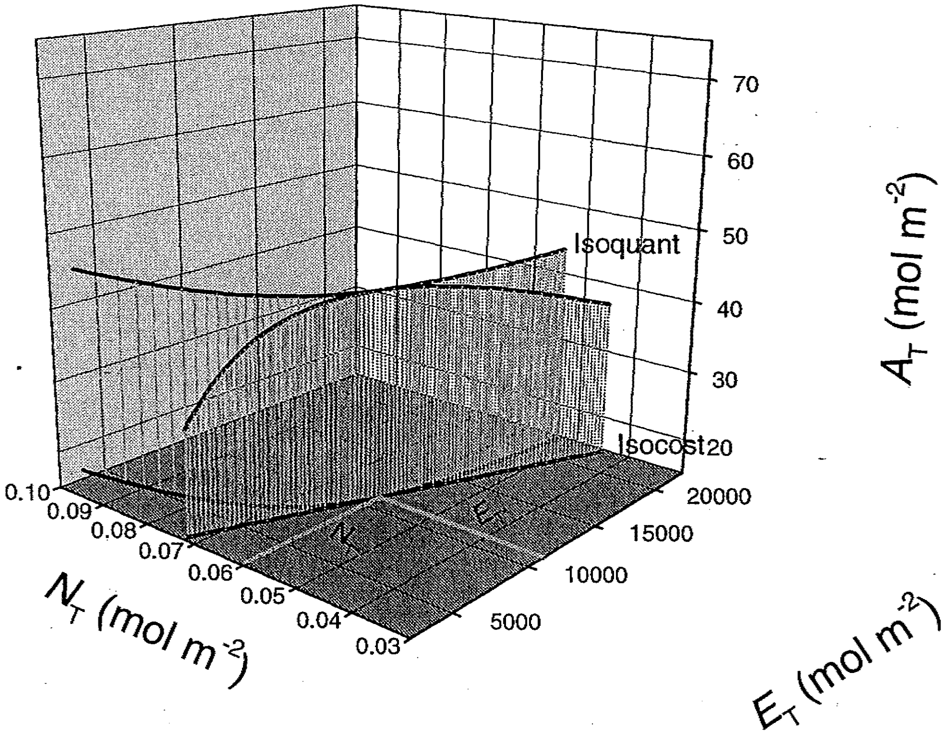

Isoquant
Isocost
70
60
50
40
30
20
A_T (mol m^{-2})
0.10
0.09
0.08
0.07
0.06
0.05
0.04
0.03
N_T (mol m^{-2})
N_T
E_T
20000
15000
10000
5000
E_T (mol m^{-2})

Figure 4.2

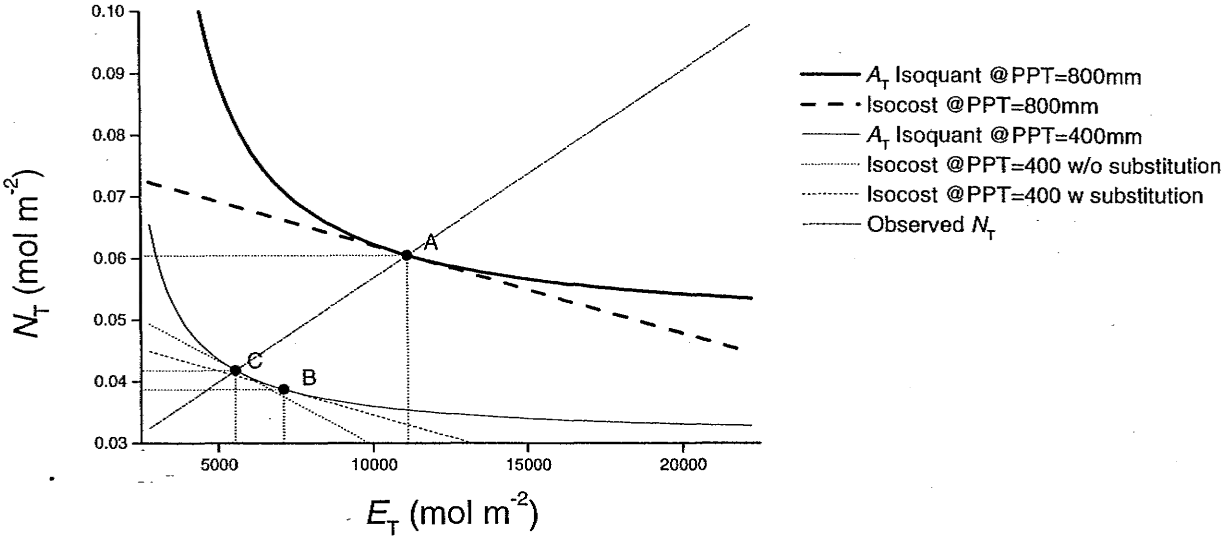
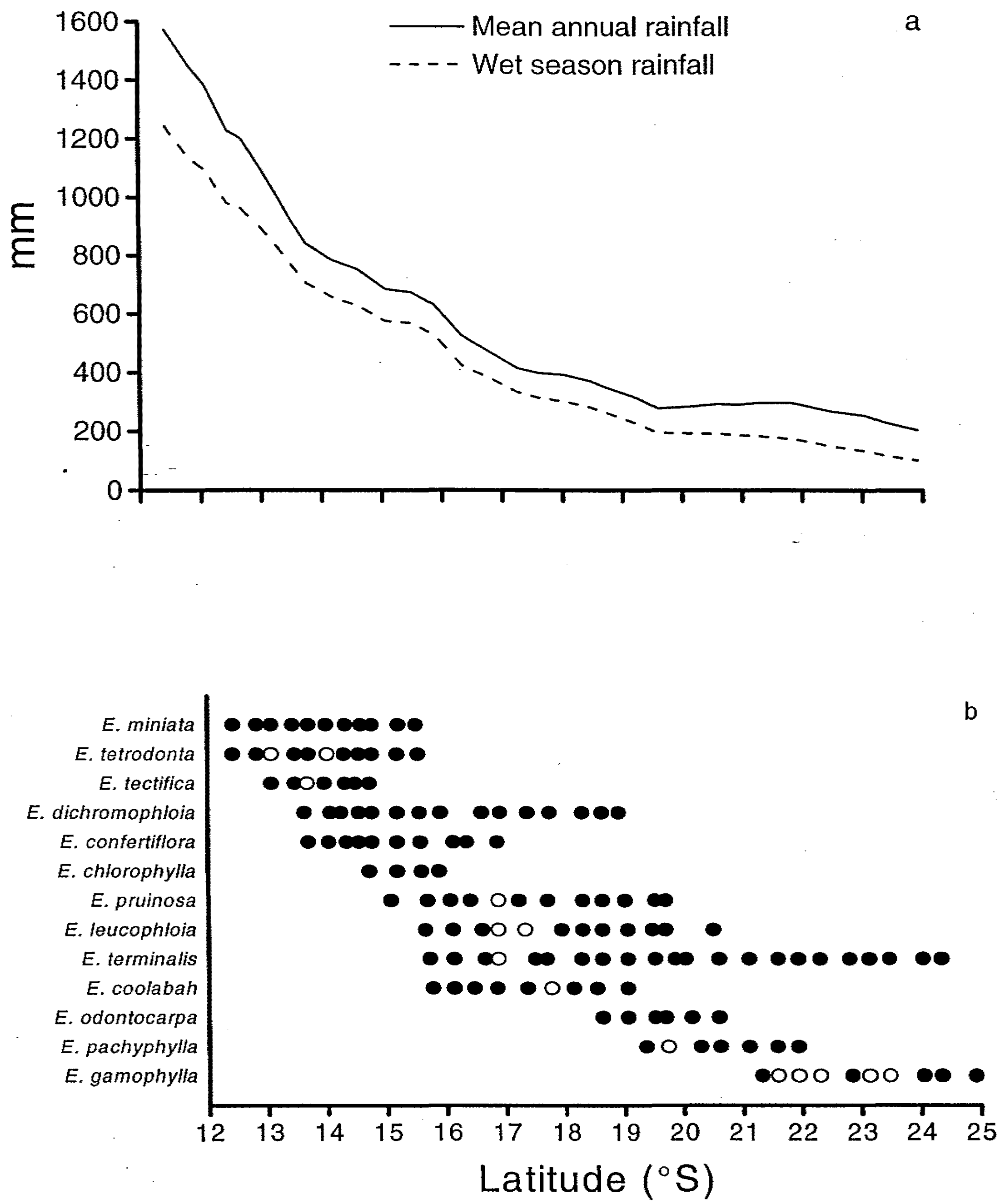

0.10
0.09
0.08
0.07
0.06
0.05
0.04
0.03
N_T (mol m^{-2})
5000
10000
15000
20000
E_T (mol m^{-2})
A
B
C
A_T Isoquant @PPT=800mm
Isocost @PPT=800mm
A_T Isoquant @PPT=400mm
Isocost @PPT=400 w/o substitution
Isocost @PPT=400 w substitution
Observed N_T

Figure 4.3



a
Mean annual rainfall
Wet season rainfall
mm
1600
1400
1200
1000
800
600
400
200
0
b
E. miniata
E. tetrodonta
E. tectifica
E. dichromophloia
E. confertiflora
E. chlorophylla
E. pruinosa
E. leucophloia
E. terminalis
E. coolabah
E. odontocarpa
E. pachyphylla
E. gamophylla
12
13
14
15
16
17
18
19
20
21
22
23
24
25
Latitude (°S)

Figure 4.4

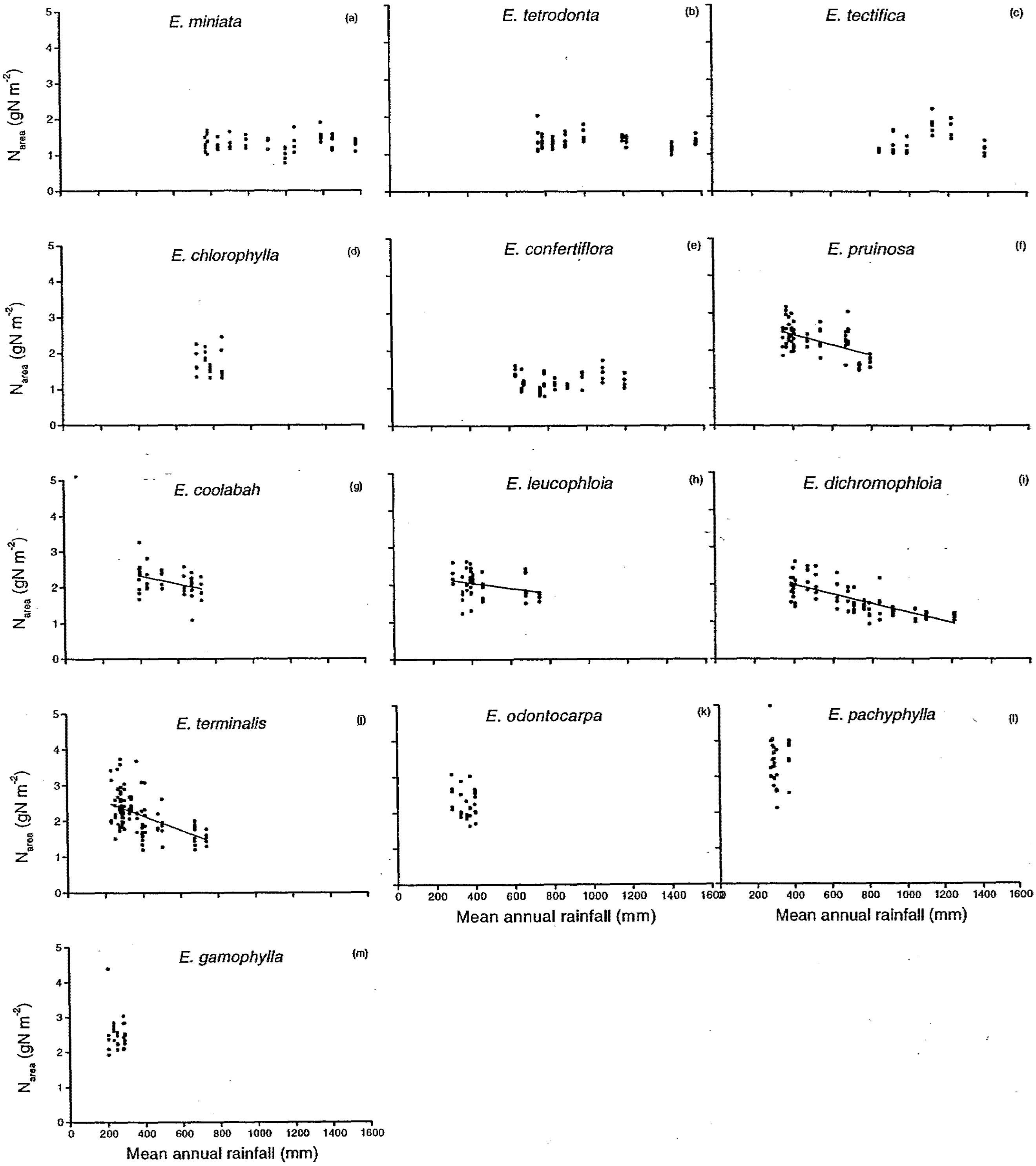

E. miniata
(a)
E. tetrodonta
(b)
E. tectifica
(c)
E. chlorophylla
(d)
E. confertiflora
(e)
E. pruinosa
(f)
E. coolabah
(g)
E. leucophloia
(h)
E. dichromophloia
(i)
E. terminalis
(j)
E. odontocarpa
(k)
E. pachyphylla
(l)
E. gamophylla
(m)
N_area (gN m^-2)
0
1
2
3
4
5
0
200
400
600
800
1000
1200
1400
1600
Mean annual rainfall (mm)

Figure 4.5

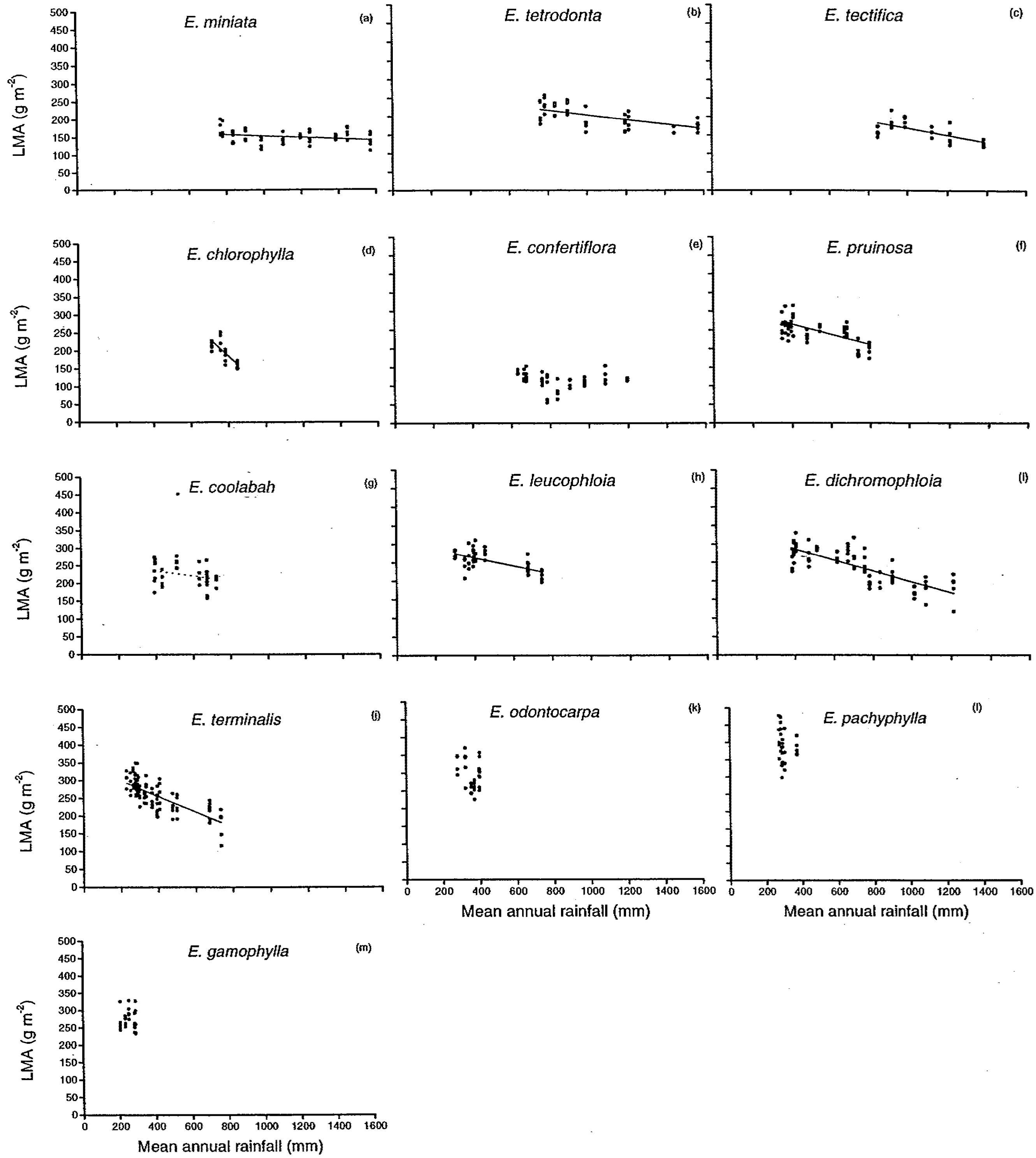
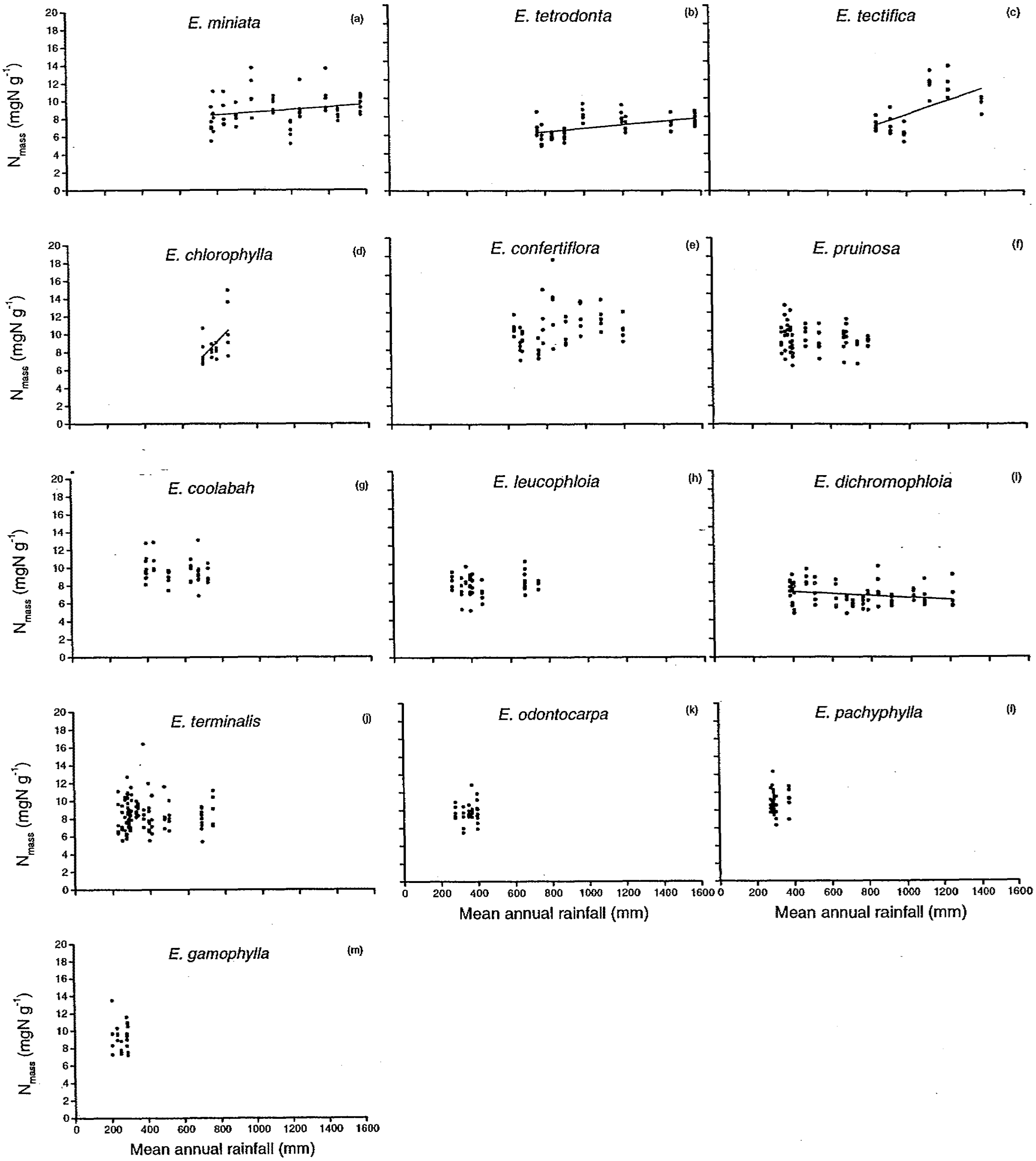

E. miniata (a)
E. tetrodonta (b)
E. tectifica (c)
E. chlorophylla (d)
E. confertiflora (e)
E. pruinosa (f)
E. coolabah (g)
E. leucophloia (h)
E. dichromophloia (i)
E. terminalis (j)
E. odontocarpa (k)
E. pachyphylla (l)
E. gamophylla (m)
LMA (g m-2)
0
50
100
150
200
250
300
350
400
450
500
Mean annual rainfall (mm)
0
200
400
600
800
1000
1200
1400
1600

Figure 4.6



E. miniata (a)
E. tetrodonta (b)
E. tectifica (c)
E. chlorophylla (d)
E. confertiflora (e)
E. pruinosa (f)
E. coolabah (g)
E. leucophloia (h)
E. dichromophloia (i)
E. terminalis (j)
E. odontocarpa (k)
E. pachyphylla (l)
E. gamophylla (m)
N_{mass} (mgN g^{-1})
0
2
4
6
8
10
12
14
16
18
20
0
200
400
600
800
1000
1200
1400
1600
Mean annual rainfall (mm)

Figure 4.7

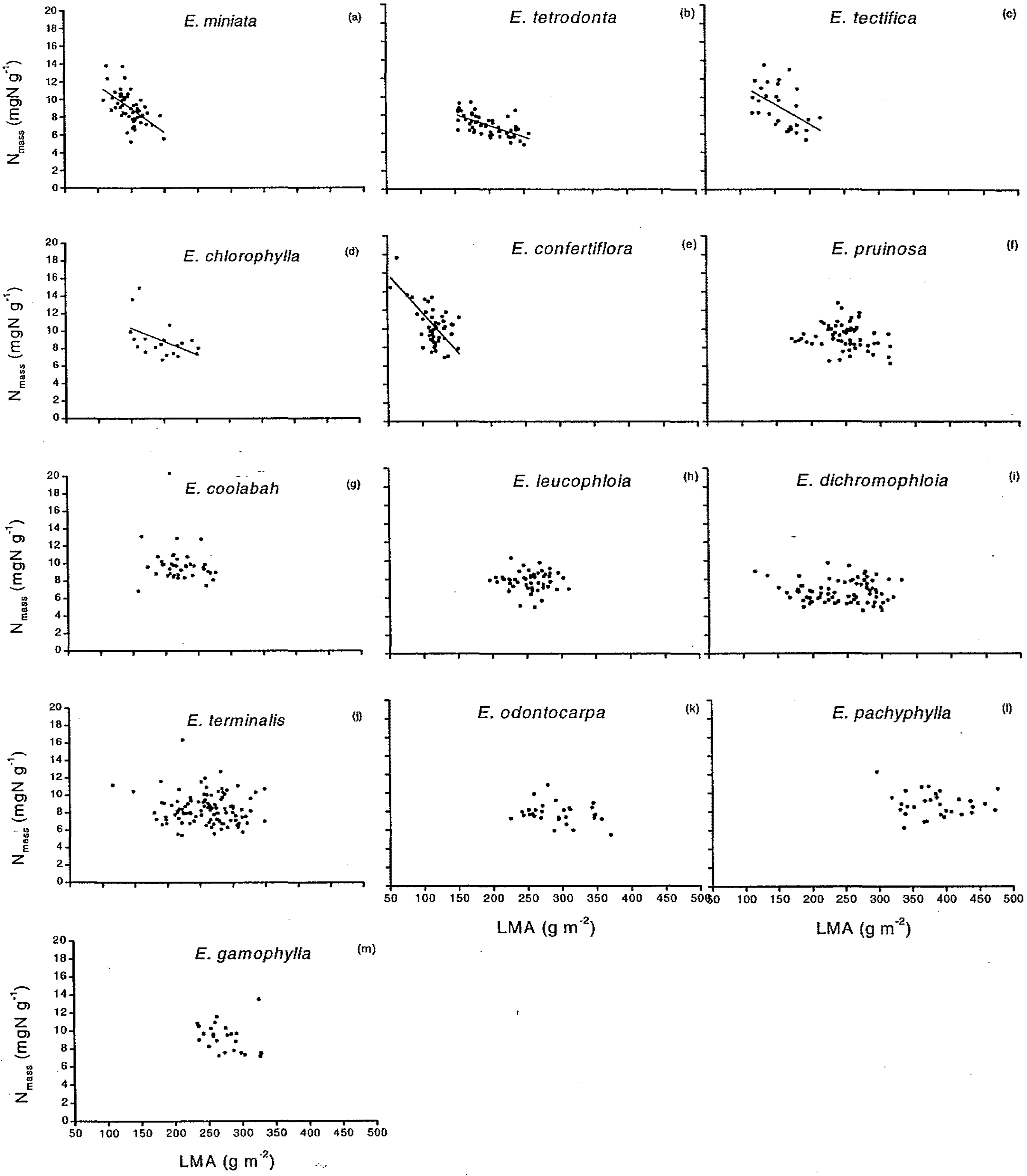

E. miniata (a)
E. tetrodonta (b)
E. tectifica (c)
E. chlorophylla (d)
E. confertiflora (e)
E. pruinosa (f)
E. coolabah (g)
E. leucophloia (h)
E. dichromophloia (i)
E. terminalis (j)
E. odontocarpa (k)
E. pachyphylla (l)
E. gamophylla (m)
N_{mass} (mgN g^{-1})
0 2 4 6 8 10 12 14 16 18 20
50 100 150 200 250 300 350 400 450 500
LMA (g m^{-2})

Figure 4.8

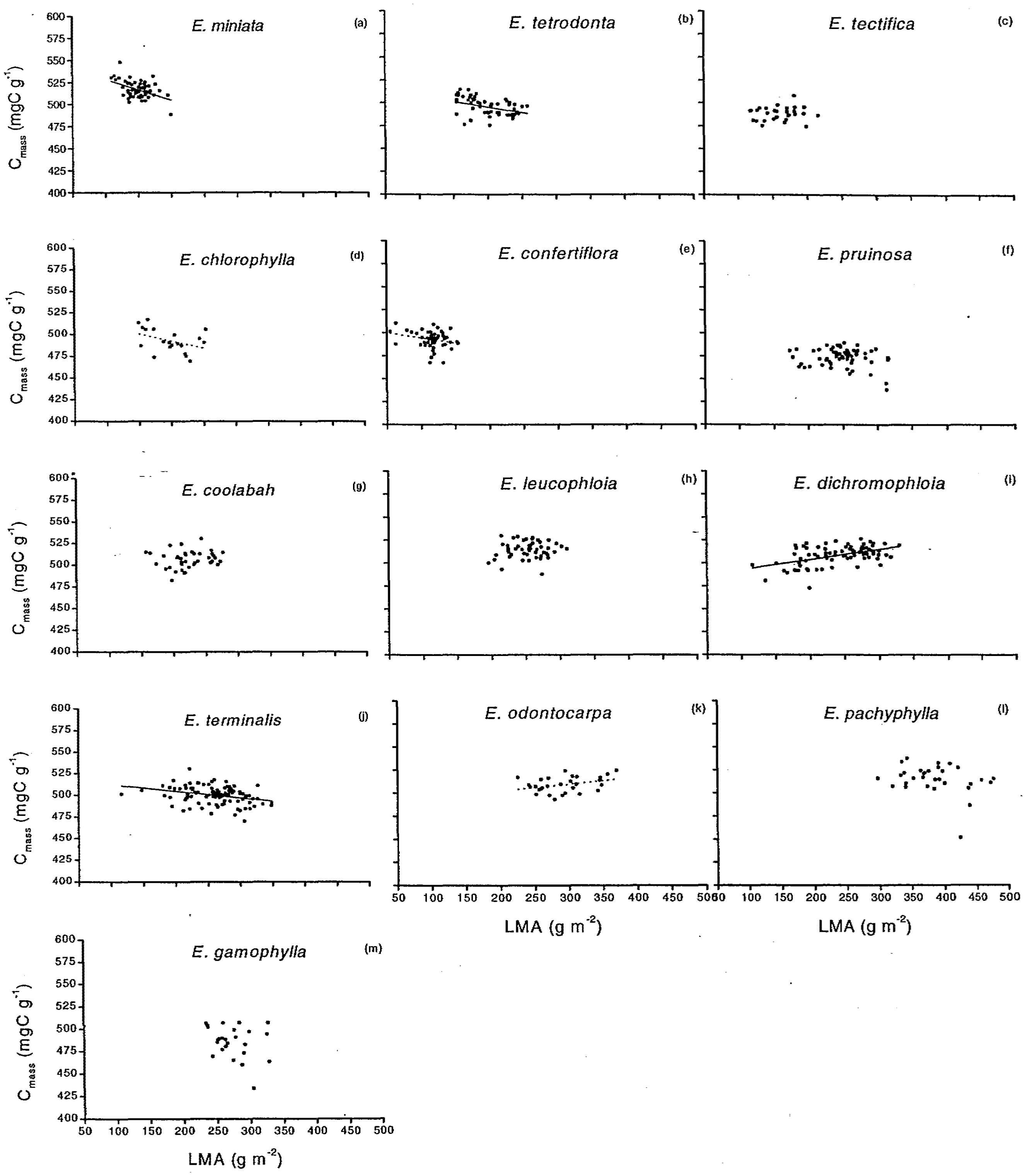

E. miniata (a)
E. tetrodonta (b)
E. tectifica (c)
E. chlorophylla (d)
E. confertiflora (e)
E. pruinosa (f)
E. coolabah (g)
E. leucophloia (h)
E. dichromophloia (i)
E. terminalis (j)
E. odontocarpa (k)
E. pachyphylla (l)
E. gamophylla (m)
C_{mass} (mgC g^{-1})
600
575
550
525
500
475
450
425
400
50
100
150
200
250
300
350
400
450
500
LMA (g m^{-2})

Figure 4.9

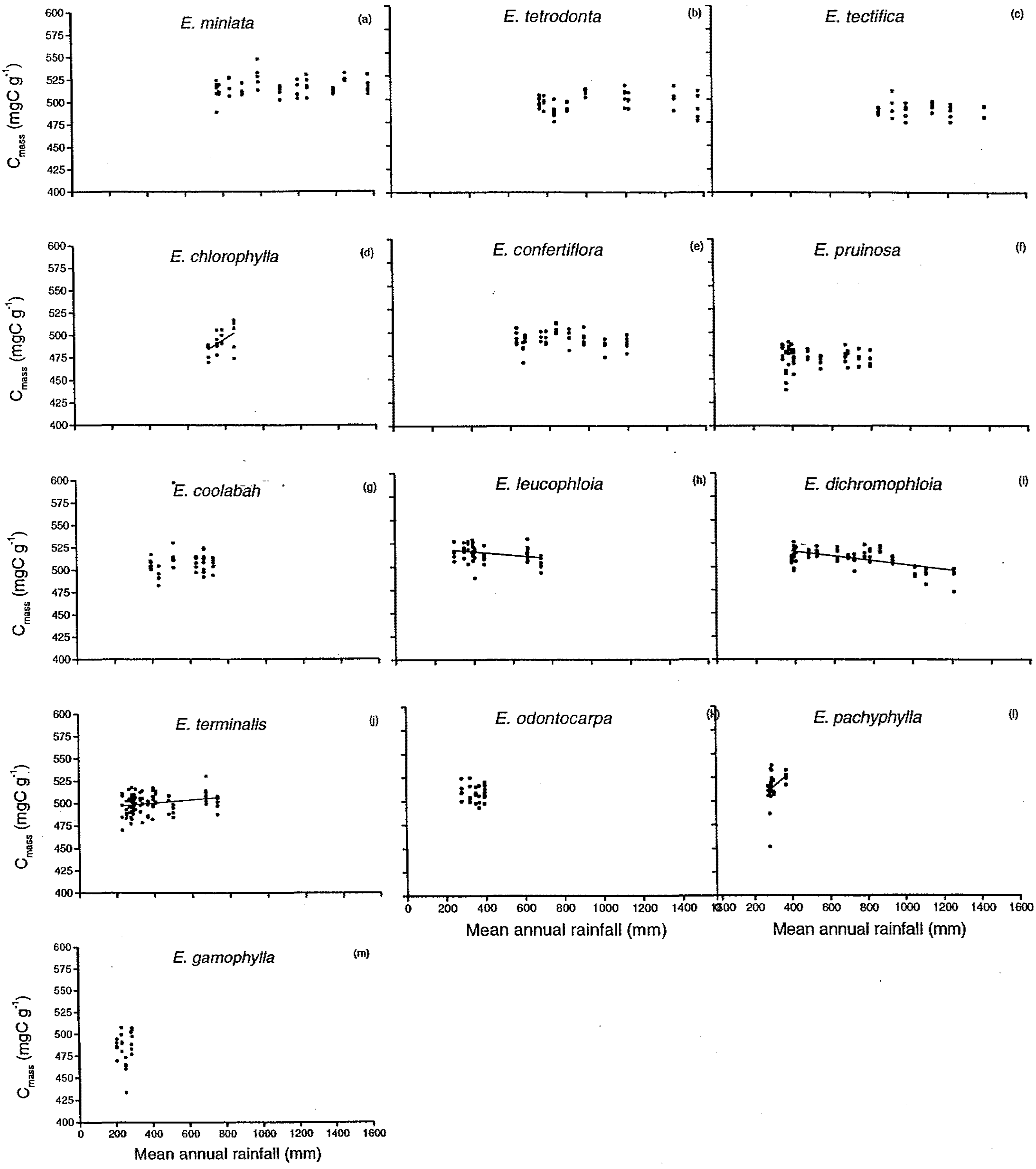

E. miniata
(a)
E. tetrodonta
(b)
E. tectifica
(c)
E. chlorophylla
(d)
E. confertiflora
(e)
E. pruinosa
(f)
E. coolabah
(g)
E. leucophloia
(h)
E. dichromophloia
(i)
E. terminalis
(j)
E. odontocarpa
(k)
E. pachyphylla
(l)
E. gamophylla
(m)
C_{mass} (mgC g^{-1})
600
575
550
525
500
475
450
425
400
0
200
400
600
800
1000
1200
1400
1600
Mean annual rainfall (mm)

Figure 4.10

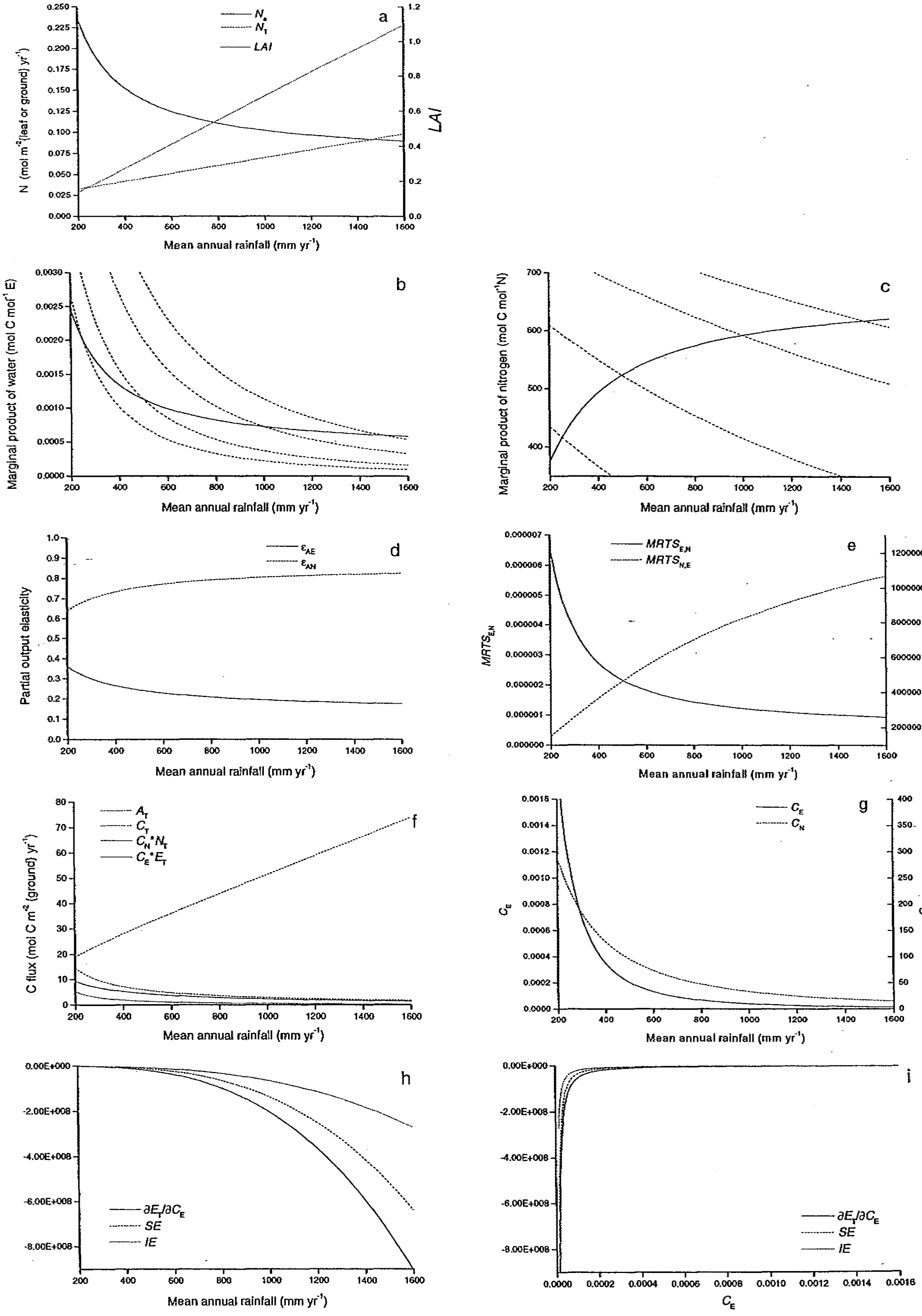

a
N_a
N_T
LAI
N (mol m^{-2}(leaf or ground) yr^{-1})
LAI
Mean annual rainfall (mm yr^{-1})
b
Marginal product of water (mol C mol^{-1} E)
Mean annual rainfall (mm yr^{-1})
c
Marginal product of nitrogen (mol C mol^{-1}N)
Mean annual rainfall (mm yr^{-1})
d
ε_{AE}
ε_{AN}
Partial output elasticity
Mean annual rainfall (mm yr^{-1})
e
$MRTS_{E,N}$
$MRTS_{N,E}$
Mean annual rainfall (mm yr^{-1})
f
A_T
C_T
$C_N{}^*N_T$
$C_E{}^*E_T$
C flux (mol C m^{-2} (ground) yr^{-1})
Mean annual rainfall (mm yr^{-1})
g
C_E
C_N
Mean annual rainfall (mm yr^{-1})
h
$\partial E_T/\partial C_E$
SE
IE
Mean annual rainfall (mm yr^{-1})
i
$\partial E_T/\partial C_E$
SE
IE
C_E

Figure 4.11

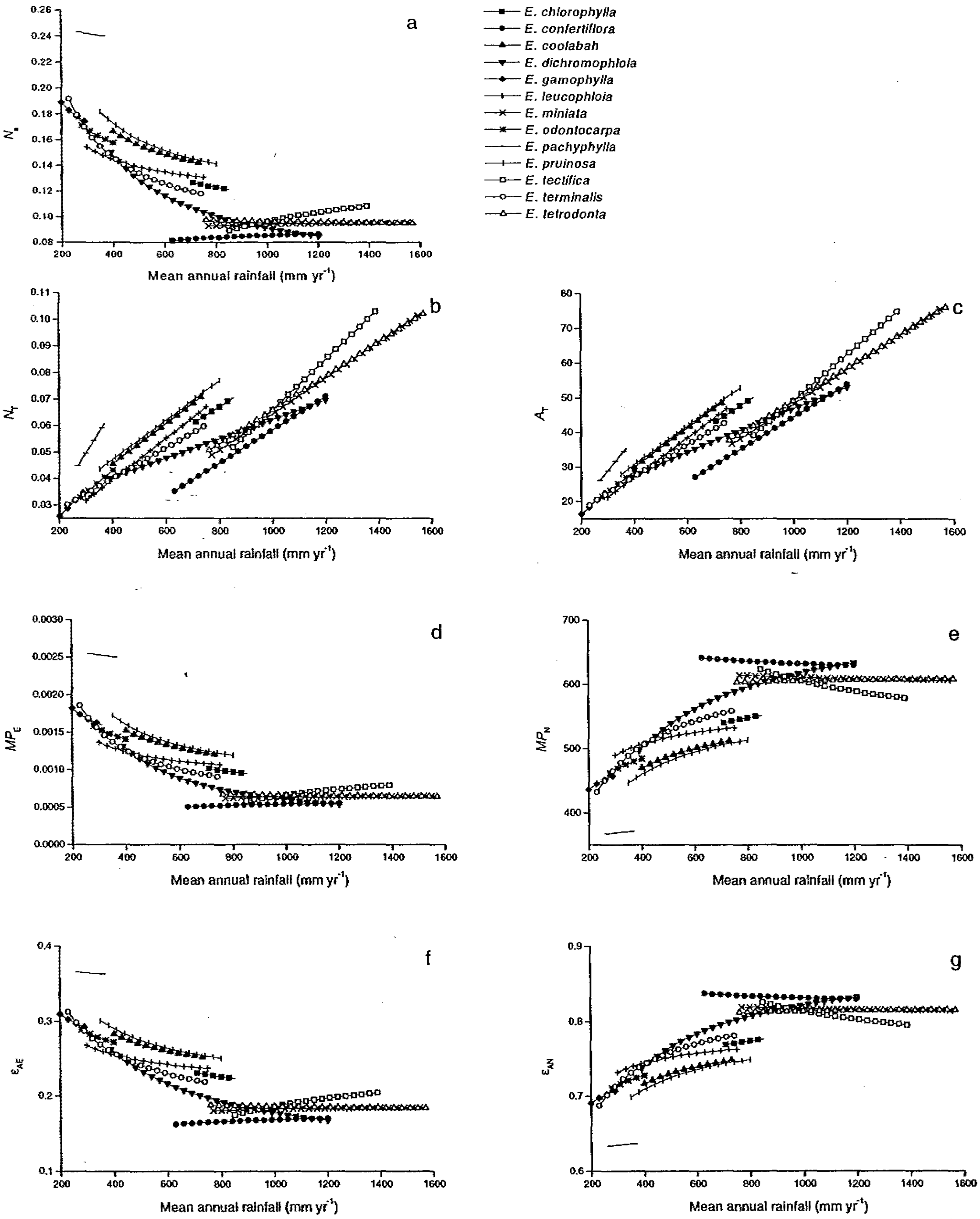

a
b
c
d
e
f
g
E. chlorophylla
E. confertiflora
E. coolabah
E. dichromophloia
E. gamophylla
E. leucophloia
E. miniata
E. odontocarpa
E. pachyphylla
E. pruinosa
E. tectifica
E. terminalis
E. tetrodonta
N_e
N_T
A_T
MP_E
MP_N
ε_{AE}
ε_{AN}
0.26
0.24
0.22
0.20
0.18
0.16
0.14
0.12
0.10
0.08
0.11
0.10
0.09
0.08
0.07
0.06
0.05
0.04
0.03
80
70
60
50
40
30
20
0.0030
0.0025
0.0020
0.0015
0.0010
0.0005
0.0000
700
600
500
400
0.4
0.3
0.2
0.1
0.9
0.8
0.7
0.6
200
400
600
800
1000
1200
1400
1600
Mean annual rainfall (mm yr^{-1})

Figure 4.12

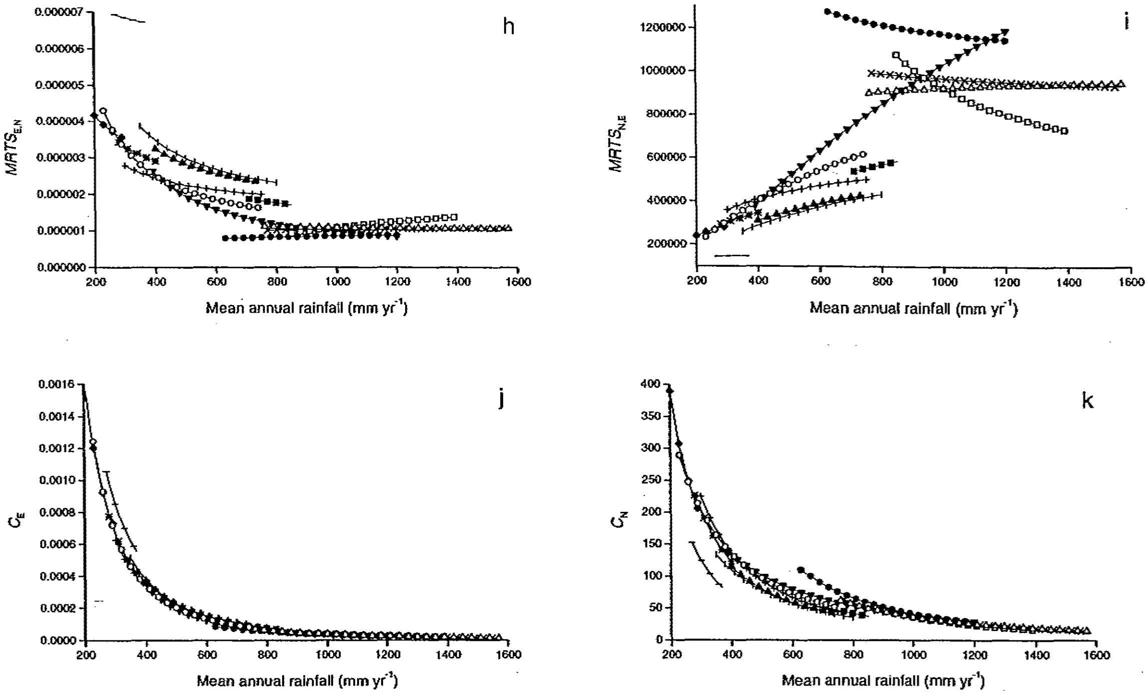


Figure 4.12 (continued)

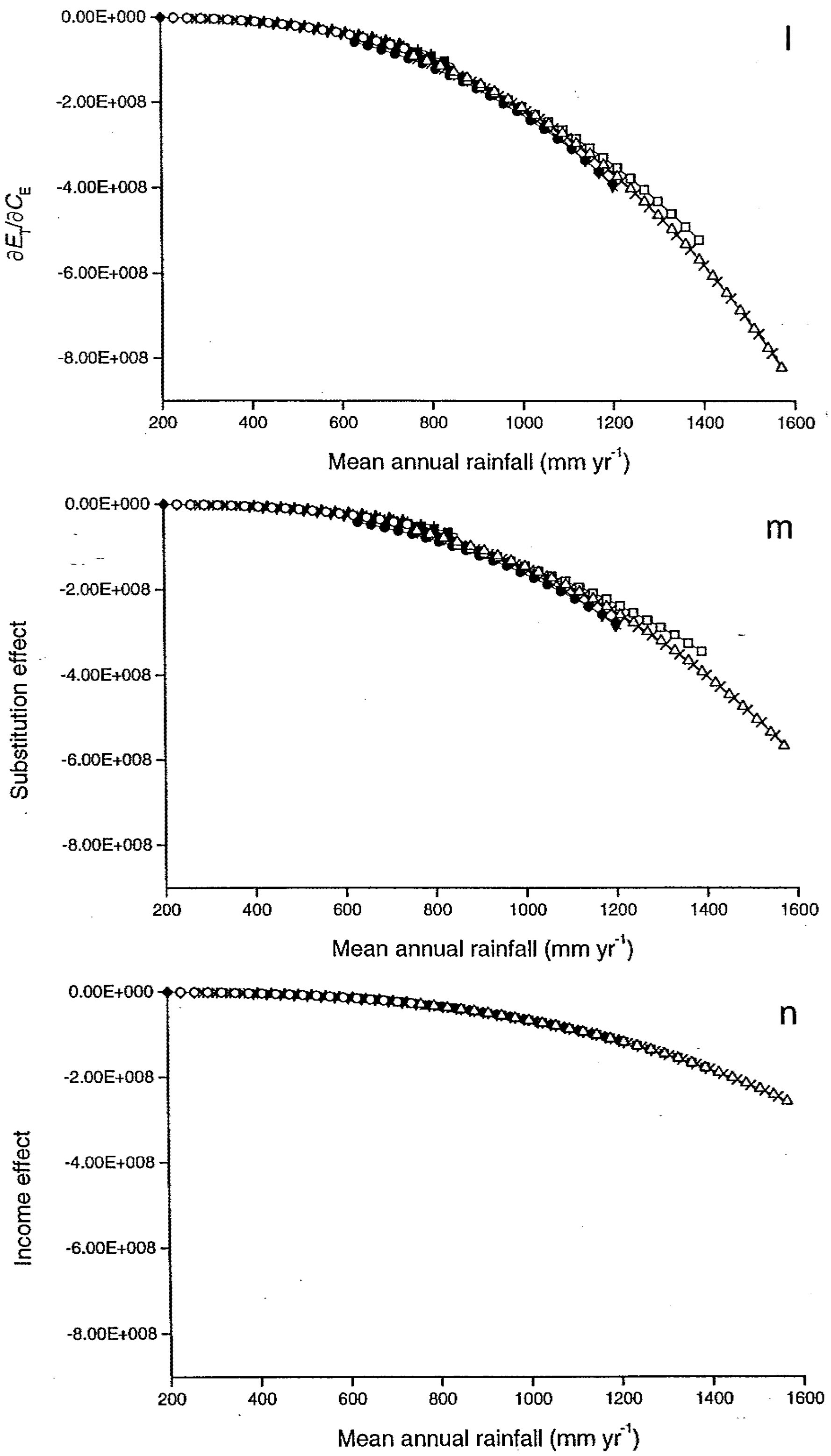


Figure 4.12 (continued)

Chapter 5

Using carbon isotope discrimination, leaf nitrogen concentration, and specific leaf area data to estimate continental-scale ecophysiologically important gas exchange parameters

Summary

1. Photosynthetic capacities were calculated from leaf nitrogen contents following Reich *et al.* (1998) for a series of co-occurring and replacement *Eucalyptus* species across an 8-fold rainfall gradient in the Northern Territory, Australia.

2. The minimum leaf payback periods were calculated from the photosynthetic capacities, the leaf mass per unit area, and the leaf carbon concentrations. The payback periods increased with decreasing rainfall across the distributions of all but one of the tree species, but not in the multi-stemmed mallee shrub species.

3. Leaf conductances, transpiration rates, and then the potential maximum supportable leaf area index were calculated from the photosynthetic capacities and leaf Δ values. The potential maximum leaf area index of all but one of the species decreased with decreasing total annual rainfall.

4. The consistent changes in leaf payback period and maximum LAI, when there were not consistent patterns in leaf Δ, indicate patterns of carbon allocation and investment may be more important than leaf level physiological performance in determining plant carbon balance and the distributions of the sampled species.

5.1 Introduction

Chapter 3 found that the carbon isotope discrimination (Δ) values recorded in the leaf tissue of dominant *Eucalyptus* species along an 8-fold rainfall gradient in the Northern Territory of Australia decreased with decreasing rainfall (Miller, Williams & Farquhar 2001). This represents a decrease in the long-term average intercellular CO_2 partial pressures (p_i) during photosynthesis. Decreases in p_i could result from either increasing stomatal limitation on photosynthesis (A), or from increased photosynthetic capacity at similar leaf conductances (g) (Richards & Condon 1993) with decreasing rainfall. The consequence of both mechanisms will be increased water-use efficiency (assuming a constant evaporative demand; D) due to the saturating response of A with increasing g, and the increasing response of E with increasing g (Farquhar, O'Leary & Berry 1982; Farquhar & Richards 1984).

The ecological implications of the two mechanisms are quite different. If decreasing patterns of Δ reflect decreasing g with constant A, then Δ gives an indication that the decreasing water supply is causing increasing stomatal limitation on photosynthesis. Lower Δ would therefore indicate increasing plant strain in response to the environmental stress of decreasing water availability and poorer performance when analyzing the relative performance of individuals across their distributions or between two co-occurring species.

If decreases in Δ reflect selection for increased photosynthetic capacity and g is not decreasing, then the pattern of decreasing Δ with decreasing rainfall reflects a growth strategy beneficial for survival rather than a measure of physiological limitation. Plants would probably have to be investing more toward root growth and N uptake, therefore allowing higher leaf N contents and photosynthetic capacity as water supply decreased. Interpreting the observed patterns in Δ, as either signs of increasing water stress limitations on carbon gain or as adaptations to increase the photosynthetic capacity relative to leaf conductance (i.e. increase the intrinsic water-use efficiency), therefore requires a measure of the magnitude of either A or g. Once either is known the other can be predicted from Δ values since

$$\Delta = a + (b - a)\left(1 - \frac{1.6AP}{g\,p_{\mathrm{a}}}\right) \qquad \text{(Eq. 5.1)}$$

where a is the discrimination against ^{13}C during diffusion through the stomata, b is the discrimination against ^{13}C by Rubisco, p_{a} is the ambient CO_2 partial pressure, and P is the total atmospheric pressure following the model of Farquhar *et al.* (1982) for the discrimination against ^{13}C during photosynthesis.

Long-term, integrated measures of gas exchange parameters over large spatial scales are difficult to directly measure. The relationship between leaf N content and photosynthetic capacities has received considerable attention and has been refined by the inclusion of specific leaf area to give robust estimates across a wide range of species and growth forms (Reich et al. 1998). As shown in Chapter 4, area-based leaf N contents increased with decreasing mean annual rainfall in the tree species in the drier half of the transect, but not in either the tree species in the wetter areas nor in the mallee growth-form species. Leaf-mass per unit area increased with decreasing mean annual rainfall in all of the tree species (except the completely drought deciduous species), resulting in decreasing or constant mass-based leaf N concentrations.

Increases in leaf mass per unit area (LMA) have been reported in response to decreases in water availability as well as to decreases in nutrient availability. The anatomical features causing the increase in LMA may vary. Low water availability may cause increased strengthening near the leaf venation, while low nutrition results in epidermal lignification, presumably as an anti-herbivore defense (Cunningham, Summerhayes & Westoby 1999). The carbon investment in each individual leaf affects the total leaf area a tree is able to create, and the amount of time required for the photosynthetic capacity of the leaf to recover its construction costs.

The aims of this Chapter were therefore to calculate photosynthetic capacities based on the leaf nitrogen contents first presented in Chapter 4, and then leaf conductances from these assimilation rates and leaf Δ values first presented in Chapter

3. Transpiration rates based on these leaf conductances can be used to estimate leaf area indices, both of which were assumed in earlier Chapters. Finally, leaf payback period can be calculated to see if it may indicate potential environmental constraints on physiology which would explain distributional patterns of the species along the rainfall gradient.

Continental scale estimates of gas exchange parameters developed from the relatively easily measured leaf nitrogen contents and carbon isotope discrimination values may prove useful in large scale bio-geochemical budgeting and modeling exercises in the study of climate change. These more integrative measures should provide an alternative to estimates from short term spot measurements of leaf gas exchange.

5.2 Methods

The study area was along a 1750 km section of the Stuart Highway between Darwin (~ 12 ½°S) and the southern border of the Northern Territory (~ 25°S). This transect was divided into 33 zones, each about 50 km long. Dominant *Eucalyptus* species with mapped distributions (Brooker & Kleinig 1994) were selected *a priori* to include species restricted to the wetter northern end of the transect (*E. miniata* A.Cunn. Ex Schauer, *E. tetrodonta* F.Muell., and *E. tectifica* F.Muell.), species with distributions starting and ending in the middle of the transect (*E. chlorophylla* Brooker&Done, *E. confertiflora* F.Muell., *E. pruinosa* Schauer, *E. coolabah* Blakely&Jacobs subsp. *coolabah*, *E. leucophloia* Brooker subsp. *QQ*, and *E. dichromophloia* F.Muell.), and species restricted to the drier southern end of the transect (*E. terminalis* F.Muell., *E. odontocarpa* F.Muell., *E. pachyphylla* F.Muell., and *E. gamophylla* F.Muell.). The species that occurred in each zone were sampled once per zone for leaf Δ (as described in Chapter 3 and Miller et al. (2001)), SLA, leaf nitrogen (on both a mass- and area-basis; N_{mass}, N_{area} as described in Chapter 4), and leaf carbon concentration (C_{mass}) at locations where they were locally abundant. From the GPS positions recorded in the field and the elevations predicted from a digital elevation map of Australia, relevant mean climatological parameters were predicted for the locations where sampling occurred using ANUCLIM 1.8 (Centre for Resource and Environmental Studies, ANU).

Mass-based net photosynthetic capacities (A_{mass}; nmol g^{-1} s^{-1}), and area-based net photosynthetic capacities (A_{area}; µmol m^{-2} s^{-1}) were calculated from the relationships between A and specific leaf area and leaf nitrogen concentration (on either a mass or area basis as appropriate) as described by Reich *et al.* (1998). Calculated A_{mass} was found with the equation that included the SLA x N interaction:

$$\log_{10}(A_{mass}) =$$
$$-2.03 + 2.019 \log_{10}(N_{mass}) + 1.433 \log_{10}(SLA) - 0.551 \log_{10}(N_{mass}) \log_{10}(SLA) \qquad \text{(Eq. 5.2)}$$

A_{area} was calculated from:

$$\log_{10}(A_{area}) = -0.51 + 0.844 \log_{10}(N_{area}) + 0.626 \log_{10}(SLA). \qquad \text{(Eq. 5.3)}$$

Conductance (g; mmol m^{-2} s^{-1}) was calculated from A_{area} and leaf Δ as

$$g = \frac{1.6 A_{area}(b-a)}{c_a(b-\Delta)} \qquad \text{(Eq. 5.4)}$$

where a = 4.4‰ and is the discrimination against ^{13}C during diffusion through the stomata, b = 27.0‰ due to the discrimination by Rubisco, and the ambient CO_2 concentrations (c_a) were assumed to be 350 ppm following the model of Farquhar *et al.* (1982) for the discrimination against ^{13}C during photosynthesis. It should be noted that these calculations cause all of the variability in leaf Δ that can not be explained by A_{area}, to be assigned to g, as g has not been independently estimated or measured.

Transpiration (E; mmol m^{-2} s^{-1}) as calculated from g and the afternoon saturated vapor pressure deficit (D; kPa) as

$$E = g\, {}^{D}\!/_{P} \qquad \text{(Eq. 5.5)}$$

where D was calculated as the difference between the saturated vapor pressures (p_v) of the 15h00 air and dew point temperatures predicted by ANUCLIM 1.8 following Campbell (1986);

$$D = e^{52.57633 - \frac{6790.4985}{T_{dry}} - 5.02808 \ln T_{dry}} - e^{52.57633 - \frac{6790.4985}{T_{dew}} - 5.02808 \ln T_{dew}} \qquad \text{(Eq. 5.6)}$$

where P (in Equation 5.5) is the atmospheric pressure and the temperatures (in Equation 5.6) are in °K.

The instantaneous water-use efficiency (A/E) was calculated as the ratio of $\mathrm{A}_{\mathrm{area}}$ to E. The time required for the assimilation rate to generate the carbon in the leaves (payback period in days) was calculated from the leaf carbon concentration and the mass-based assimilation rate assuming it continued at a constant rate during an 8 hour day;

$$Payback = \frac{\left(\frac{\mathrm{C}_{\mathrm{mass}}}{12\mathrm{x}10^{-6} A_{\mathrm{mass}}} \right)}{60 \text{ x } 60 \text{ x } 8}. \qquad \text{(Eq. 5.7)}$$

The potential maximum leaf area index was calculated from the ratio of the total annual rainfall and the annual transpiration rate which was found by assuming the average of the monthly E values occurred consistently for 8 hour days all through the year;

$$LAI = \frac{PPT}{18 \text{ x } E_{\bar{\mathrm{x}}} \text{ x } 60 \text{ x } 60 \text{ x } 8 \text{ x } 365 \text{ x } 10^{-6}}. \qquad \text{(Eq. 5.8)}$$

where PPT is precipitation (mm/yr). When this leaf area index was applied to a single species it assumed all of the incident rainfall was transpired through the canopy of that single species in question. When it was applied to all of the overstorey species it assumed a mixed canopy of equal numbers of the sampled species. There was no allowance made for runoff, drainage, or the presence of the understorey.

5.3 Results

The zone-mean values of leaf Δ were presented in Chapter 3 (Figure 3.3) and are re-presented here as scatter-plots of the actual data in response to increasing rainfall (Figure 5.1). The response of N_{mass} across the gradient (Figure 4.7) is repeated here (Figure 5.3) for completeness. The inverse of leaf mass per unit area (LMA) (Figure 4.6) is presented, since SLA (Figure 5.2) was used to calculate the photosynthetic capacities.

Leaf Δ

E. miniata and *E. tetrodonta* are the co-dominant species defining many of the vegetation types north of around 15°S along this transect. *E. miniata* had higher calculated gas exchange parameters than *E. tetrodonta*, both in terms of carbon gain and water loss, leading to lower calculated water-use efficiency. *E. miniata* showed patterns of Δ that indicated a greater sensitivity to the increasing environmental stresses from north to south across the distribution of the species than *E. tetrodonta*. The leaf Δ of *E. miniata* declined significantly from around 21.7‰ to 20.5‰ with decreasing rainfall (Figure 5.1a). The leaf Δ of *E. tetrodonta*, in contrast, showed no clear trend with decreasing rainfall, and was around 20.4‰ (Figure 5.1b).

E. tectifica and *E. chlorophylla* are two very similar appearing species with narrow, non-overlapping distributions. Their limited ranges, especially in the case of *E. chlorophylla* which was found in only four zones, made accurately representing trends across their distribution difficult. It would seem that both species showed little trend with decreasing rainfall in leaf Δ, but the changes in SLA and N_{mass} caused changes in calculated *A* parameters. The differences between the two species, which would explain their disjunct distributions, were not clear. The leaf Δ of both species tended to increase toward the drier south, although the trend was not significant in the case of *E. tectifica* and leaf Δ values of both species were between 20 and 21.5‰ (Figures 5.1c and 5.1d).

E. confertiflora was the only completely dry-season deciduous species sampled. All of the measured and calculated parameters, except the calculated water-use efficiency, showed no trends with decreasing rainfall. Only extremely young leaves were available to be sampled in the middle of the distribution of the species, and they had distinctive SLA and N_{mass} values which then affected the calculated A_{mass} values. Leaf Δ values of *E. confertiflora* averaged 19.9‰ (Figure 5.1e).

E. pruinosa, *E. coolabah*, and *E. leucophloia* were three species distributed in the center of the transect, from around 15 to 21 °S. *E. pruinosa* and *E. leucophloia* were sampled over wide latitudinal ranges (between 4½ and 5½° latitude), and *E. coolabah* was sampled over an intermediate range (between 2½ and 3½° latitude). Most of the measured and calculated parameters of the three species placed them in the middle of the ranked list of the 13 species. In most parameters *E. pruinosa* and *E. coolabah* were not separable, while *E. leucophloia* was lower. The leaf Δ of *E. pruinosa* and *E. leucophloia* significantly decreased with decreasing rainfall (Figures 5.1f and 5.1 h). Leaf Δ of *E. pruinosa* dropped from ~ 21.4‰ to ~19.0‰ and that of *E. leucophloia* dropped from ~20.2‰ to ~17.6‰ . Leaf Δ values of *E. coolabah* varied between 18.4 and 20.6‰ (Figure 5.1g).

The combined distributions of *E. dichromophloia* and *E. terminalis* covered over 90% of the entire transect, with *E. terminalis* being present in all but the wettest 15% of the 33 sampled zones. *E. dichromophloia* exhibited trends with decreasing rainfall in all of the measured and calculated parameters calculated *g*. The leaf Δ of both species significantly decreased with decreasing rainfall (Figures 5.1i and 5.1j). The end points of the linear regressions of the leaf Δ values of *E. dichromophloia* showed a drop from 20.9 to 19.8‰ across the range of the species, and the leaf Δ values of *E. terminalis* were around 20.1‰ in the north and dropped to ~18.2‰ in the south.

The three multi-stemmed mallee shrubs *E. odontocarpa*, *E. pachyphylla*, and *E. gamophylla* were restricted to the drier, southern end of the transect. The three species had the lowest SLA values of the sampled *Eucalyptus* species, the lowest leaf Δ of all the species, and were among the lowest in terms of A_{mass} and *g*. The Δ values across the restricted distribution of each of the three species showed no significant trends (Figures 5.1k, 5.1l, and 5.1m). Leaf Δ of the three species averaged around 17.5‰ .

SLA

The specific leaf area of *E. miniata* and *E. tetrodonta* significantly declined with decreasing rainfall (Figures 5.2a and 5.2b). The SLA of *E. miniata* was consistently higher than that of *E. tetrodonta*; averaging between 6.3 and 7.2 m^2 kg^{-1} versus between 4.5 and 5.8 m^2 kg^{-1} (based on the endpoints of the linear regressions). The SLA of *E. tectifica* and *E. chlorophylla* decreased by around 30% across their distributions, with the SLA of *E. tectifica* dropping from around 8 to 5.5 m^2 kg, and that of *E. chlorophylla* dropping from about 6 to 4 m^2 kg (Figures 5.2c and 5.2d).

E. confertiflora had the highest SLA of all the species measured. The specific leaf areas of *E. confertiflora* averaged between 7.5 and 9.5 m^2 kg^{-1} in most of the 10 zones comprising the distribution of the species, except where only very young leaves were sampled which had SLA values averaging between 11 and 12 m^2 kg^{-1} (Figure 5.2e).

Within a zone the specific leaf area of *E. pruinosa*, *E. coolabah*, and *E. leucophloia* showed little variability (Figures 5.2f, 5.2g, and 5.2h). There were significant decreases in SLA with decreasing rainfall in *E. pruinosa* and *E. leucophloia*, from ~5 to ~4m^2 kg^{-1} and ~4.5 to ~3.5m^2 kg^{-1}, while the SLA of *E. coolabah* averaged 4.5 m^2 kg^{-1} across it's distribution.

The SLA of *E. dichromophloia* dropped from near 6 to about 3.7 m^2 kg^{-1} between 13½°S and 16°S and then stayed near 3.7 m^2 kg^{-1} until 19°S (Figure 5.2i). The SLA of *E. terminalis* consistently declined across the complete distribution of the species, from ~4.9 to ~3.1 m^2 kg^{-1} (Figure 5.2j). The average SLA values of *E. odontocarpa*, *E. pachyphylla*, and *E. gamophylla* were 3.5, 2.6, and 3.7 m^2 kg^{-1} respectively (Figures 5.2k, 5.2l, and 5.2m).

N_{mass} and C_{mass}

The leaf nitrogen concentrations of *E. miniata* were significantly higher than those of *E. tetrodonta* on a mass-basis, and averaged around 9 versus 7 mgN g^{-1} for all samples (Figures 5.3a and 5.3b). There were significant decreases in N_{mass} with decreasing rainfall for both species; from around 9.6 to 8.2 mgN g^{-1} in the case of *E. miniata*, and from around 7.7 to 6.1 mgN g^{-1} in the case of *E. tetrodonta* (based on the end points of the linear regressions). The higher N_{mass} of *E. miniata* was offset by a higher SLA, so both species had area-based N concentrations (N_{area}) of around 1.3 gN m^{-}

^{2} which did not change with decreasing rainfall. The higher SLA of *E. miniata*, compared to *E. tetrodonta*, did not come from a lower carbon concentration in the leaves; *E. miniata* averaged around 517 mg C g^{-1} while *E. tetrodonta* had around 495 mg C g^{-1}, and neither species showed any variability with decreasing rainfall (Figure 4.10).

Leaf N_{mass} of both *E. tectifica* and *E. chlorophylla* were significantly higher in the wetter north than in the drier south, but over all both averaged around 8.9 mgN g^{-1} (Figures 5.3c and 5.3d). In both species the N_{mass} values did not seem to vary continuously with decreasing rainfall, but instead were between 9 and 12 mgN g^{-1} in the north or between 6 and 8 mgN g^{-1} in the south. The differences in SLA meant N_{area} of *E. tectifica* was around 1.4 gN m^{-2} while that of *E. chlorophylla* was around 1.7 gN m^{-2} and neither showed a trend with decreasing rainfall. The leaf carbon concentrations of *E. tectifica* were around 490 mgC g^{-1} and showed no trend with decreasing rainfall while those of *E. chlorophylla* dropped significantly from around 500 to 485 mgC g^{-1} with decreasing rainfall (Figure 4.10).

E. confertiflora had the highest average N_{mass} of the *Eucalyptus* species sampled ($\bar{x}$: 10.4 mgN g^{-1}) (Figure 5.3e), and the lowest average N_{area} ($\bar{x}$: 1.2 gN m^{-2}) of all the species. The leaf carbon concentrations were not unique, and averaged about 490 mgC g^{-1} (Figure 4.10).

Leaf N_{mass} of *E. pruinosa* and *E. coolabah* averaged 9.1 and 9.6 mgN g^{-1}, while that of *E. leucophloia* was 7.8 mgN g^{-1} (Figures 5.3f, 5.3g, and 5.3h). None of the three species exhibited significant trends in N_{mass} with decreasing rainfall. In contrast to the lack of trends of N_{mass}, N_{area} increased significantly in all three species from north to south across their distributions. N_{area} in *E. pruinosa* varied (based on the end points of the linear regressions) from ~1.9 to ~2.6 gN m^{-2}, and in *E. coolabah* between ~2.0 and ~2.4 gN m^{-2}, while in *E. leucophloia* the range was smaller, between ~1.8 and ~2.1 gN m^{-2}. Leaf carbon concentrations of *E. pruinosa* and *E. coolabah* showed no trend with decreasing rainfall and averaged about 473 and 506 mgC g^{-1} respectively (Figure 4.10). Leaf carbon concentrations of *E. lecuophloia* showed a slight, but significant increase with decreasing rainfall from ~509 to ~518 mgC g^{-1}.

Leaf nitrogen concentrations of *E. dichromophloia* on a mass- and area-basis both increased significantly with decreasing rainfall; N_{mass} from 6.2 to 7.1 mgN g^{-1}, and N_{area}

from 1.1 to 2.1 gN m^{-2} (Figure 5.3i). N_{mass} values of *E. terminalis* were rather variable, and showed no trend with decreasing rainfall and averaged 8.4 mgN g^{-1} (Figure 5.3j). The changes in SLA meant N_{area} significantly increased with decreasing rainfall from 1.7 to 2.6 gN m^{-2}. Leaf carbon concentrations in *E. dichromophloia* increased from ~490 to ~510 mgC g^{-1} as rainfall decreased from around 1200 to 900 mm yr^{-1}, and then remained at ~510 mgC g^{-1} over the rest of the species range to rainfalls of about 400 mm yr^{-1} (Figure 4.10). In *E. terminalis* the C_{mass} values declined slightly, but significantly, from just over to just under 500 mgC g^{-1} from north to south.

Neither the N_{mass} nor the N_{area} of *E. odontocarpa*, *E. pachyphylla*, or *E. gamophylla* varied with decreasing rainfall (Figures 5.3k, 5.3l, and 5.3m). N_{mass} of *E. odontocarpa*, *E. pachyphylla*, and *E. gamophylla* averaged 7.8, 8.8, and 9.2 mgN g^{-1}, and N_{area} averaged 2.3, 3.4, and 2.5 gN m^{-2}. The N_{mass} values of these three species were indistinguishable from those of the other species that were measured, but the N_{area} values were the highest of the *Eucalyptus* values measured. The average C_{mass} value of *E. pachyphylla* was nearly the highest measured at 515 mgC g^{-1}, just lower than *E. miniata* at 517 mgC g^{-1}, and there was no trend in C_{mass} with decreasing rainfall (Figure 4.10). *E. odontocarpa* and *E. gamophylla* also showed no trend in C_{mass} with decreasing rainfall, and averaged 509, and 486 mgC g^{-1}. The average C_{mass} of *E. gamophylla* was the second lowest measured.

A_{mass}

The calculated net photosynthetic capacity on a mass-basis (calculated A_{mass}) of *E. miniata* was consistently higher than that of *E. tetrodonta* (averages of about 37 versus 22 nmol g^{-1} s^{-1}), and both species exhibited significant declines with decreasing rainfall (Figures 5.4a and 5.4b). The higher SLA of *E. miniata* did not counteract the calculated A_{mass}, and the calculated area-based net photosynthetic capacity (calculated A_{area}) of *E. miniata* was also significantly higher than that of *E. tetrodonta* (Figures 5.5a and 5.5b), although there were less noticeable trends in calculated A_{area} with decreasing rainfall. The calculated photosynthetic nitrogen-use efficiency (calculated A_N) of *E. miniata* was higher than that of *E. tetrodonta*, and declined in both species with decreasing rainfall.

The patterns of calculated A_{mass} of *E. tectifica* and *E. chlorophylla* reflected their patterns of N_{mass}; at the wetter, northern 3 sites where *E. tectifica* was sampled the calculated A_{mass} values were around 45 nmol g^{-1} s^{-1} and at the drier, southern three sites they were around 25 nmol g^{-1} s^{-1}, while the calculated A_{mass} values of *E. chlorophylla* were about 40 nmol g^{-1} s^{-1} at the wettest site and 20 nmol g^{-1} s^{-1} at the southern 3 sites (Figures 5.4c and 5.4d). This pattern carried through to the calculated A_{area} values for both species, with *E. tectifica* having values between 5.5 and 7 µmol m^{-2} s^{-1} at the wetter sites and 4.5 to 5 µmol m^{-2} s^{-1} at the drier sites (Figure 5.5c). The variability in the calculated A_{area} values of *E. chlorophylla* at the wetter site resulted in a non-significant trend with decreasing rainfall (Figure 5.5d). The calculated A_{area} values of *E. chlorophylla* were between 6.5 µmol m^{-2} s^{-1} in the north and 5.5 µmol m^{-2} s^{-1} in the south. The calculated A_N decreased significantly with decreasing rainfall in both species, from around 4.5 to about 3.3 µmol gN^{-1} s^{-1} in *E. tectifica* and from around 3.7 to about 2.6 µmol gN^{-1} s^{-1} in *E. chlorophylla.*

The calculated A_{mass} values of *E. confertiflora* reflected the patterns of SLA, with extremely high values (averaging between 80 and 90 nmol m^{-2} s^{-1}) in two zones, and the other zones averaging between 40 and 60 nmol m^{-2} s^{-1} (Figure 5.4e). Calculated A_{mass} averaged 55 nmol m^{-2} s^{-1} overall, which was much higher than the second ranked species, *E. miniata*, which had an average calculated A_{mass} of 36 nmol m^{-2} s^{-1}. Calculated A_{area} averaged 5.8 µmol m^{-2} s^{-1} (Figure 5.5e). The average calculated A_N of *E. confertiflora* (5.1 µmol gN^{-1} s^{-1}) was much higher than the second ranked species, *E. miniata* (4.0 µmol gN^{-1} s^{-1}).

The calculated A_{mass} of *E. pruinosa* averaged 23.4 nmol g^{-1} s^{-1} and that of *E. coolabah* 27.1 nmol g^{-1} s^{-1}, and neither varied significantly with decreasing rainfall (Figures 5.4f and 5.4g). The calculated A_{mass} of *E. leucophloia* decreased with decreasing rainfall, and the predicted values from the linear regression were between 21.3 and 17 nmol g^{-1} s^{-1} (Figure 5.4h). The calculated A_{area} of *E. pruinosa* increased with decreasing rainfall, with the predicted values between 5.9 and 6.5 µmol m^{-2} s^{-1} (Figure 5.5f). Calculated A_{area} of *E. coolabah* and *E. leucophloia* did not vary significantly with decreasing rainfall and averaged 6.3 and 5.5 µmol m^{-2} s^{-1} respectively (Figures 5.5g and 5.5h). Calculated A_N of *E. pruinosa* and *E. leucophloia* decreased with decreasing rainfall, while that of *E. coolabah* showed no trend. The predicted response of A_N with decreasing rainfall in *E. pruinosa* was from 2.9 to 2.3 μmol gN^{-1} s^{-1}, while the predicted response of *E. leucophloia* was from 2.7 to 2.2 μmol gN^{-1} s^{-1}. The calculated A_N of *E. coolabah* averaged 2.8 μmol gN^{-1} s^{-1}.

The A_{mass} calculated from the SLA and N_{mass} of both *E. dichromophloia* and *E. terminalis* decreased with decreasing mean annual rainfall across the distribution of each species (Figures 5.4i and 5.4j). In *E. dichromophloia* the predicted values from the linear regression ranged from 20.6 to 14.0 nmol g^{-1} s^{-1}, while in *E. terminalis* they were between 24.9 and 17.1 nmol g^{-1} s^{-1}. The pattern in SLA reversed the trend in calculated A_{area} for the two species, and the predicted values from the regression increased from 4.2 to 5.2 μmol m^{-2} s^{-1} for *E. dichromophloia* and from 5.5 to 6.2 μmol m^{-2} s^{-1} for *E. terminalis* with increasing decreasing rainfall (Figures 5.5i and 5.5j). The species average calculated A_{area} value of *E. dichromophloia* (4.7 μmol m^{-2} s^{-1}) was the second lowest (just above *E. tetrodonta* which also averaged 4.7 μmol m^{-2} s^{-1}). The calculated A_N of both species decreased with decreasing rainfall; from 3.2 to 1.9 μmol gN^{-1} s^{-1} for *E. dichromophloia*, and from 3.0 to 2.0 μmol gN^{-1} s^{-1} for *E. terminalis*.

There was no trend with decreasing rainfall in calculated A_{mass} for *E. odontocarpa*, *E. pachyphylla*, or *E. gamophylla* (Figures 5.4k, 5.4l, and 5.4m). The average calculated A_{mass} values of *E. odontocarpa* (16.7 nmol g^{-1} s^{-1}) and *E. pachyphylla* (15.0 nmol g^{-1} s^{-1}) were the lowest of the 14 species in this study, while *E. gamophylla* averaged 21.5 nmol g^{-1} s^{-1}. Calculated A_{area} values for the three species also showed no trends with decreasing rainfall (Figures 5.5k, 5.5l, and 5.5m). The average calculated A_{area} values of *E. pachyphylla* (6.6 μmol m^{-2} s^{-1}) and *E. gamophylla* (6.4 μmol m^{-2} s^{-1}) were the highest of the *Eucalyptus* species, while *E. odontocarpa* (5.6 μmol m^{-2} s^{-1}) was a middle ranked species. The average calculated A_N values of *E. odontocarpa*, *E. pachyphylla*, and *E. gamophylla* were 2.1, 1.7, and 2.3 μmol gN^{-1} s^{-1} respectively, and were the lowest of all of the sampled species.

c_i

The internal CO_2 concentrations calculated from the Δ values ranged from just over 180 ppm to just under 300 ppm (Figure 5.6). This represents a range in c_i/c_a from 0.52 to 0.84. The patterns in the calculated c_i values directly follow those of the Δ values. The variability in the c_i values that is not explained by the patterns of the calculated A_{area} (which depend on N_{area} and SLA) are reflected in the patterns of the calculated leaf conductances.

g

The calculated leaf conductances (to water vapour) of *E. miniata* were significantly higher than the calculated values of *E. tetrodonta* (Figures 5.7a and 5.7b). The calculated leaf conductances of *E. miniata* declined with decreasing rainfall from about 110 to 80 mmol m^{-2} s^{-1}, while those of *E. tetrodonta* were unchanged south of the northern-most site, and averaged 75 mmol m^{-2} s^{-1}. From the monthly average afternoon vapor pressure deficits and the calculated leaf conductances, it would seem that the transpiration rates of *E. miniata* were higher than those of *E. tetrodonta* (Figures 5.8a and 5.8b), and the water-use efficiency of *E. miniata* was lower than that of *E. tetrodonta* (Figures 5.9a and 5.9b). The sharp decline in calculated g with decreasing rainfall of *E. miniata* did not offset the increased VPD, and both species showed significant increases in calculated E with decreasing rainfall, and significant decreases in calculated A_{area}/E. The time required for the calculated A_{mass} to generate the measured C_{mass} (i.e. the leaf payback period) increased in both species from north to south across their distributions (Figures 5.10a and 5.10b). In *E. miniata* the values (based on the end points of the linear regressions) varied between 37 and 52 days, while the leaf payback period of *E. tetrodonta* increased from 53 to 90 days.

The calculated leaf conductances of *E. tectifica* were around 70 mmol m^{-2} s^{-1} except at 2 sites where they were between 100 and 125 mmol m^{-2} s^{-1} (Figure 5.7c). The calculated g of *E. chlorophylla* averaged about 100 mmol m^{-2} s^{-1} across the distribution of the species (Figure 5.7d). The calculated transpiration patterns of both species tracked the patterns of calculated g, with the northern 3 sites where *E. tectifica* was sampled exhibiting distinctly different values from about 1.7 to 3.7 mmol m^{-2} s^{-1}, while the southern 3 sites were very similar with values about 2.3 mmol m^{-2} s^{-1} (Figure 5.8c). The calculated E values of *E. chlorophylla* were all around 3.3 mmol m^{-2} s^{-1} (Figure 5.8d). The calculated water-use efficiency of both species decreased from north to south, with the values of *E. tectifica* between 3 and about 1.7 mmol mol^{-1}, while the values of *E. chlorophylla* were between 2 and 1.6 mmol mol^{-1} (Figures 5.9c and 5.9d). The patterns in the leaf payback periods of *E. tectifica* and *E. chlorophylla* reflected the patterns of A_{mass} of the two species (Figures 5.10c and 5.10d). In the northern 3 zones were *E. tectifica* was sampled leaf payback periods averaged 32 days, while in the southern 3 zones the average was 62 days. Leaf payback periods of *E. chlorophylla* varied between 40 and 68 days based on the end points of the linear regression.

The calculated *g* values of *E. confertiflora* averaged 86 mmol m^{-2} s^{-1} which placed the species 7th of the 13 species (Figure 5.7e). The calculated transpiration values were highest in the middle of the distribution of the species, and averaged 2.8 mmol m^{-2} s^{-1} overall (Figure 5.8e). The calculated water-use efficiency decreased with decreasing rainfall from 2.3 to 1.9 mmol mol^{-1} (Figure 5.9e). The leaf payback period of *E. confertiflora* was significantly shorter than all of the other sampled species and showed a slight trend with decreasing rainfall from 25 to 35 days (Figure 5.10e).

The calculated *g* of *E. pruinosa* and *E. leucophloia* decreased with decreasing rainfall (Figures 5.7f and 5.7h). The predicted values, based on the linear regression, of calculated *g* for *E. pruinosa* were between ~110 and ~83 mmol m^{-2} s^{-1}, while the values for *E. leucophloia* were between ~83 and ~60 mmol m^{-2} s^{-1}. The calculated *g* of *E. coolabah* did not vary with decreasing rainfall and averaged 88 mmol m^{-2} s^{-1} (Figure 5.7g). The calculated *E* of *E. pruinosa* and *E. leucophloia* significantly decreased with decreasing rainfall, while it significantly increased in *E. coolabah* (Figures 5.8f, 5.8g, and 5.8h). The predicted values of *E* for *E. pruinosa* dropped from 3.7 to 3.1 mmol m^{-2} s^{-1}, while those for *E. leucophloia* dropped from 2.9 to 2.2 mmol m^{-2} s^{-1}. The predicted valued for *E* of *E. coolabah* increased from 2.9 to 3.4 mmol m^{-2} s^{-1}. The calculated ratio of A_{area} to *E* increased with decreasing rainfall for *E. pruinosa*, from 1.6 to 2.1 mmol mol^{-1}, and *E. leucophloia*, from 1.9 to 2.5 mmol mol^{-1}, and had no trend for *E. coolabah*, averaging 2.1 mmol mol^{-1} (Figures 5.9f, 5.9g, and 5.9h). The leaf payback periods of *E. pruinosa* and *E. coolabah* were very similar, while those of *E. leucophloia* were slightly longer (Figures 5.10f, 5.10g, and 5.10h). Based on the values from the linear regressions, the leaf payback period of *E. pruinosa* increased from 55 to 67 days while that of *E. leucophloia* increased from 72 to 89 days. *E. coolabah* exhibited no trend in leaf payback period with decreasing rainfall and averaged 56 days.

The calculated g showed no trends with decreasing rainfall for both *E. dichromophloia* and *E. terminalis*, and averaged 74 mmol m^{-2} s^{-1} for *E. dichromophloia* and 78 mmol m^{-2} s^{-1} for *E. terminalis* (Figures 5.7i and 5.7j). The calculated patterns of transpiration of both species exhibited significant changes with decreasing rainfall (Figures 5.8i and 5.8j). The predicted values (based on the linear regression) of the calculated E of *E. dichromophloia* increased from 2.2 to 2.8 mmol m^{-2} s^{-1}. North of ~20°S, which was about the southern limit of *E. dichromophloia*, the calculated E of *E. terminalis* also tended to increase, but further the south it decreased, so the overall trend was a reduction in calculated E with decreasing rainfall. The calculated water-use efficiency of *E. dichromophloia* showed no trend with decreasing rainfall and averaged 1.9 mmol mol^{-1}, while the predicted values (based on the linear regression) of the calculated A_{area}/E of *E. terminalis* increased from 1.7 to 2.8 mmol mol^{-1} with decreasing rainfall (Figures 5.9i and 5.9j). The calculated leaf payback periods of both of the species were highly variable within zones and between adjacent zones (Figures 5.10i and 5.10j). In both species the leaf payback period increased with decreasing rainfall, from 77 to 108 days in the case of *E. dichromophloia*, and from 64 to 86 days in the case of *E. terminalis* (based on the end points of the linear regressions).

The calculated g values of *E. odontocarpa*, *E. pachyphylla*, and *E. gamophylla* showed no trends with decreasing rainfall (Figures 5.7k, 5.7l, and 5.7m). The average calculated g values of *E. odontocarpa*, and *E. gamophylla* (63 and 71 mmol m^{-2} s^{-1}) were the lowest two measured. The average calculated g of *E. pachyphylla* was 74 mmol m^{-2} s^{-1}. Calculated transpiration of *E. odontocarpa* and *E. gamophylla* showed no trends with decreasing rainfall (averaging 2.3 and 2.2 mmol m^{-2} s^{-1}), while that of *E. pachyphylla* decreased from 2.8 to 2.3 mmol m^{-2} s^{-1}, based on the linear regression values (Figures 5.8k, 5.8l, and 5.8m). The calculated instantaneous water-use efficiencies of *E. odontocarpa* and *E. pachyphylla* increased with decreasing rainfall from 2.3 to 2.6 mmol mol^{-1} and 2.3 to 2.9 mmol mol^{-1}, based on the respective linear regressions, while that of *E. gamophylla* showed no trend and averaged 3.0 mmol mol^{-1} (Figures 5.9k, 5.9l, and 5.9m). The A_{area}/E ratios of the tree species were the highest of all of the sampled species. The leaf payback periods of *E. pachyphylla* and *E. odontocarpa* were the longest of all of the sampled species, with that of *E. pachyphylla* being significantly different from all of the other species (Figures 5.10k, 5.10l, and

5.10m). None of the tree species exhibited any trends in leaf payback period with decreasing rainfall. The leaf payback periods of *E. odontocarpa*, *E. pachyphylla*, and *E. gamophylla* averaged 93, 104, and 69 days.

LAI

If all of the incident precipitation was transpired and there were no other pathways for water to leave the soil, the maximum supportable leaf area indices would be below 4 at most sites by most species across the transect (Figure 5.11). The strong gradient in rainfall would decrease the potential maximum LAI supportable by all species across their distributions except for *E. pachyphylla*. None of the species show patterns of reduction in water-use, i.e. reductions in g or E, which would allow them to escape having to make morphological adjustments as a consequence of the decrease in water availability across their distributions.

Inter-species comparisons

The relationships between the regression lines describing the responses of the 13 species to decreasing rainfall gives an indication of the patterns of their responses and their position along the transect (Figure 5.12). As described in detail in Chapter 3, the leaf Δ values of species in the wetter areas declined less steeply with deceasing rainfall than those of species in the drier areas (Figure 5.12a). The most obvious difference from the general trends are the increasing leaf Δ values of *E. chlorophylla* which was found in the middle of the rainfall gradient.

The specific leaf areas of the single completely drought deciduous species that was sampled, *E. confertiflora*, were generally higher than those of co-occurring species (Figure 5.12b). Much of this difference was due to the fact that only very young leaves were available to be sampled in many areas, which may have also contributed to the variability in the leaf Δ and N_{mass} values of the species. The SLA values of *E. pachyphylla* also stand out as being lower than the general trend of the other species.

The trends in N_{mass} with decreasing rainfall for all the species are slight and similar, except that of *E. chlorophylla* (Figure 5.12c). The importance of both patterns of N_{mass} and patterns of SLA in determining the calculated A_{mass} are demonstrated by the responses of A_{mass} of *E. confertiflora* and *E. pachyphylla* (Figure 5.12d). *E. confertiflora* had significantly higher calculated A_{mass} values than the other species primarily due to its high SLA values, while the N_{mass} values of *E. pachyphylla* countered the low SLA values such that the A_{mass} values were similar to co-occurring species. Following *E. confertiflora* in the ranking of species mean A_{mass} values were *E. miniata* and *E. tectifica*, followed by the other species which did not show significant differences in calculated A_{mass}.

The mean calculated A_{area} and calculated g values of the species were related to the position of the species along the transect (Figures 5.12e and 5.12f). *E. pruinosa*, *E. chlorophylla*, and *E. coolabah*, which had distributions in the middle of the transect where the SVPD values were highest, had the highest calculated E values, while *E. odontocarpa*, *E. gamophylla*, and *E. tetrodonta* had low values distinguishable from the other species (Figure 5.12g). The species mean instantaneous water-use efficiencies were also correlated with the position of the species along the transect (Figure 5.12h). *E. gamophylla* had significantly higher calculated A_{area}/E ratios than the other species which were harder to distinguish into groups. The ratio of the total annual rainfall to the species mean total annual transpiration gives an upper boundary for leaf area index. The low calculated E of *E. tetrodonta* in the wet northern part of the transect gave it the highest potential LAI (Figure 5.12j). The potential LAI values of *E. tectifica* and *E. miniata*, and *E. confertiflora* and *E. dichromophloia* were two distinguishable groups from those of the rest of the species. The ratio of the carbon content of the leaves to the calculated assimilation rate (both on a mass-basis) gives an estimate of the period required for the leaf to become an exporter of carbon (ignoring translocation that might occur at senescence). The species mean leaf payback period was related to the position of the species along the transect (Figure 5.12i). The deciduous *E. confertiflora* had a significantly shorter payback period than the other species. *E. dichromophloia* and *E. odontocarpa*, and lastly *E. pachyphylla* had significantly longer payback periods.

Transect zone means

If the *Eucalyptus* species that were sampled are treated as indicators of the response of the overstory vegetation, or at least as indicators of the *Eucalyptus* component of the overstory, then some general response patterns can be described (Figure 5.13). The mean values (of all species present in each zone) of most of the characters that were measured or calculated, with the exception of mass-based leaf nitrogen concentration and mass-based leaf carbon concentration (data not shown), exhibited significant trends with decreasing rainfall. The responses of many of the characters were non-linearly related to decreasing rainfall, with the complex pattern of the calculated *E* reflecting the peak in annual average SVPD values in the middle of the transect.

The zone mean leaf Δ decreased linearly with latitude, and non-linearly with decreasing rainfall (Figure 5.13a). Position along the transect accounted for 42% of the variability in the 671 samples of leaf Δ. From the north to the south there was a decrease in zone mean Δ of 3.7‰. The high variability in zone mean leaf Δ south of 21.5°S (equivalent to rainfall of around 300 mm yr^{-1}) was the result of only 1 or 2 species being present; the tall tree *E. terminalis* and the mallee shrub *E. gamophylla.*

The non-linear pattern of rainfall with latitude, coupled with the linear response of leaf Δ, meant that the relationship between Δ and rainfall was non-linear. Third-order polynomials captured the patterns of leaf Δ values with decreasing total annual rainfall. In the zones where annual rainfall was between 1600 and 1400 mm yr^{-1} there were slight decreases in leaf Δ values. Where rainfall was between 1400 and about 600 mm yr^{-1} where values were little changed. Leaf Δ values then sharply declined in the zones where total annual rainfall was between 600 and 200 mm yr^{-1}.

Zone mean specific leaf area decreased from 6 to 7 m^2 kg^{-1} in the north to between 3 and 4 m^2 kg^{-1} in the south (Figure 5.13b). The main change in SLA occurred between 15°S and 17°S which corresponds to the southern edge of the distributions of the tropically distributed species. The variability within a zone was less at sites south of 17°S where the seasonally deciduous *E. confertiflora* was no longer found.

Mass-based leaf nitrogen concentrations were constant across the transect and averaged 8.6 mg g^{-1} (Figure 5.13c). Zone average area-based nitrogen concentrations increased significantly ($P < 0.0001$) with decreasing rainfall from around 1.25 to 2.75

gN m^{-2} reflecting the changes in SLA. Zone mean leaf carbon concentrations varied little across the transect, and averaged just over 500 mgC g^{-1}.

From the specific leaf area and either the mass- or area-based leaf nitrogen concentrations, the calculated net photosynthetic capacities (on both mass- and area-bases; Reich et al. 1998) showed significant ($P<0.0001$) trends with decreasing rainfall (Figures 5.13d and 5.13e). Zone mean calculated A_{mass} decreased from between 30 and 40 nmol g^{-1} s^{-1} to around 20 nmol g^{-1} s^{-1} from north to south, while the decrease in SLA reversed the trend for calculated A_{area} which increased from around 5 to around 6 µmol m^{-2} s^{-1}. Photosynthetic nitrogen-use efficiency (A_N) values reflect the SLA values as A_{mass} was calculated from SLA and N_{mass}, and A_N was calculated from A_{mass} and N_{mass}. Zone average A_N values were around 4 µmol gN^{-1} s^{-1} in the north and decreased to around 2.5 µmol gN^{-1} s^{-1} in the south. Leaf conductances, based on the calculated A_{area} and the leaf Δ values decreased significantly ($P < 0.0001$) from around 90 to around 70 mmol m^{-2} s^{-1} (Figure 5.13f). Although there was a significant trend in calculated E (based on the calculated g and the mean mid-afternoon SVPD) with decreasing rainfall, the pattern was clearly non-linear (Figure 5.13g).

The zone mean calculated E values increased from about 2 mmol m^{-2} s^{-1} in the north to around 3 mmol m^{-2} s^{-1} at the midpoint of the transect and then dropped to slightly below 2 mmol m^{-2} s^{-1} in the south. The ratio of calculated A_{area} to calculated E (a calculated instantaneous water-use efficiency value that is similar to the ratio of Δ to SVPD due to the methods used to calculate g as a function of A_{area} and Δ) mirrored the patterns of calculated E (Figure 5.13h). Overall, there was an increase in calculated water-use efficiency with increasing decreasing rainfall. The overall response of A_{area}/E with decreasing rainfall was stronger than the response of E, but the highest values were at both ends of the transect. Converting the instantaneous E values to an annual total (with the assumption of 8 hour days) finds around 512 mm of water being transpired per unit leaf area all across the transect. The ratio of annual total rainfall to annual total transpiration gives a crude estimate of an upper bound on the leaf area index along the transect, which varied from about 4 in the north to around 0.6 for all areas south of 17°S (Figure 5.13j). The response of this upper bound on LAI was not linear, as it was determined by rainfall which distinctly decreased exponentially with latitude. The ratio of the leaf carbon content to the assimilation rate (both mass-based), gives an estimate of the time required to recover the construction costs of the leaves. Assuming 8 hour days, it would require 40 to 50 days for the species at the northern end of the transect to accumulate the carbon that was in the leaves (Figure 5.13i). The leaf payback period increased to between 70 and 100 days in the species sampled at about 21 °S, and then slightly decreased again further south.

5.4 Discussion

Leaf carbon isotope discrimination decreased with decreasing rainfall across the distributions of 5 of the 13 dominant *Eucalyptus* species sampled along a 1750 km transect with an 8-fold rainfall gradient. Leaf Δ increased in 1 species, and exhibited no consistent trend in 7 species. The decreasing trends in leaf Δ reflect decreasing stomatal conductances relative to photosynthetic demands arising from either a decreasing ability of stomatal conductance to satisfy photosynthetic demand, or increasing photosynthetic demand and constant stomatal conductances. Where there were no trends in leaf Δ, either stomatal conductances were unaffected by decreasing water supply or photosynthetic capacity and leaf conductances responded similarly (Wong, Cowan & Farquhar 1979).

The lack of consistent patterns of decreasing leaf Δ with decreasing total annual rainfall may mean that Δ can not be used as a long-term integrated measure of the stomatal limitation on photosynthesis resulting from increasing periods of water stress. Alternatively, it may mean that naturally occurring populations of overstory trees do not necessarily experience increasing periods of water stress across a spatial gradient of decreasing water availability. Since Δ measures the ratio of leaf conductance to assimilation at the level of the individual leaf, adjustment of canopy leaf area index could offset the decrease in water supply. Inferring the physiological limits on species distributions, specifically the range in total annual water supply which would allow a positive carbon balance, is not possible with measurements of Δ.

One element of the growth strategy of a plant that influences a positive total carbon balance is the time required for the assimilation capacity of the leaves to recover their construction costs, or payback period (Pearcy et al. 1987; Poorter 1994). The ratio of photosynthetic capacity to leaf carbon content gives an indication of the minimal leaf payback period, but does not include either the continuing costs of respiration or those during leaf construction. The leaf payback periods of all but one (*E. coolabah*) of the tree species significantly increased with decreasing rainfall across the distribution of each species. The variability in the calculated leaf payback periods, and the narrow distributional ranges of the three mallee shrub *Eucalyptus* species, meant significant trends could not be found.

Except for the completely dry-season deciduous species, *E. confertiflora*, all those species with significantly increasing leaf payback periods had significantly decreasing specific leaf areas (equivalent to significantly increasing leaf mass per unit area) with decreasing rainfall. Two of the species, *E. leucophloia* and *E. dichromophloia* also had significantly increasing mass-based leaf carbon concentrations with decreasing total annual rainfall, but in *E. terminalis* there was a significant decrease in leaf carbon concentration. The increasing specific leaf area could have resulted from changes in several possible leaf parameters; there could be an increase in leaf thickness, there could be a decrease in cell sizes, or there could be a decrease in the volume of the internal airspaces. Changes in each of these parameters could have differing implications for physiological performance (Roderick et al. 1999a; Roderick et al. 1999b; Roderick, Berry & Noble 1999c). Leaf mass per unit area has been found to increase along gradients of decreasing water availability and decreasing soil nutrient availability, but as the result of differing anatomical changes (Cunningham et al. 1999).

From the measured photosynthetic capacities and LMA values presented by Mooney *et al.* (1978) for 1 year old plants in pots, the payback periods can be calculated in the same way as they were here, and values between 13 and 40 days found for six species originating from across a rainfall gradient in New South Wales. Leaf construction costs and returns have been calculated for the leaves of *E. miniata* and *E. tetrodonta* near Darwin (Eamus et al. 1999), who found that longevity correlated positively with leaf construction costs.

Although the area-based leaf nitrogen contents increased in 5 species with decreasing total annual rainfall, the mass-based leaf nitrogen contents increased in only 1 species and decreased in 4 species. From the patterns of the payback periods it is clear that the changes in the mass-based leaf N concentrations give a better indication of the time required to recover the carbon costs supporting that nitrogen investment than area-based leaf N concentrations (Evans 1989; Field 1991).

Calculating the photosynthetic capacities, based on the leaf nitrogen contents and specific leaf areas allowed a large scale survey to be conducted in a limited amount of time, but may not necessarily relate well to actual assimilation rates. Actual assimilation rates would asymptotically approach the potential maximum values depending on c_i and leaf conductances, but would almost always be lower. The universality of a single regression satisfying the leaf nitrogen content - photosynthetic capacity relationship should also be tested for the dominant *Eucalyptus* species in the Northern Territory, as well as its consistency across the distribution of those species.

Carbon isotope discrimination is linearly related to intercellular CO_2 concentrations (Farquhar et al. 1982). The amount of photosynthate produced with a certain isotopic signature will weight the isotopic value of the product by both the isotopic signal and the photosynthetic rate. A product made from photosynthate from two equal time periods with a large variation in leaf conductance, one with a high conductance and high discrimination and other with a restricted conductance and low discrimination, will not be a linear average of the discrimination values of the two time periods. The saturating response of assimilation capacity with increasing c_i will bias the resulting Δ towards the period with high photosynthetic rate. This bias will underestimate the amount of time during which there was limited stomatal conductance.

Calculating leaf conductances from maximum photosynthetic capacity, rather than actual assimilation rate, and leaf Δ will consistently over estimate g. However, the predicted values of leaf conductance of the adult *E. tetrodonta* trees near Darwin were about 50% of the values reported by Eamus, Myers, Duff & Williams (1999) for trees near Darwin, and predicted values of the area-based photosynthetic capacities were about 1/3 of those reported by Eamus et al. (1999).

The calculated leaf conductances decreased across the distributions of four of the species with decreasing rainfall, but in only two species were these decreases sufficient to offset increasing SVPD values and therefore result in decreasing transpiration rates per unit leaf area. The calculated transpiration rates increased in three species with decreasing water availability, so the possibility of variation in water-use efficiency in naturally occurring populations of *Eucalyptus* species is still unresolved (*e.g.* Hatton et al. 1998).

The predicted changes in water-use per unit leaf area were not as strong as the changes in total annual rainfall, such that the potential maximum leaf area indices of 12 of the 13 species would have to significantly decrease with decreasing total annual rainfall. The differences in the pattern of leaf Δ values across the transect and calculated instantaneous water-use efficiency (*A*/*E*) are due to the changing evaporative demand (Chapter 6), and point out that Δ is not a measure of water-use efficiency in non-constant environments.

The consistency of the predicted decreases in maximum potential supportable leaf area per unit ground area, and of the increases in predicted time required for the assimilation capacity to recover the carbon content in the leaves point to these issues being more important in determining the distributional tolerances of the species than the ratio of leaf conductance to assimilation rate as measured by leaf Δ. The *Eucalyptus* species sampled may be ameliorating the physiological strain resulting from decreasing water availability via plasticity in morphological characters. If the carbon balance of the trees is determining their distributions then allocation patterns and investment strategies seem to be more important than leaf level physiological performance.

5.5 Literature Cited

Brooker, M.I.H. & Kleinig, D.A. (1994) Field Guide to Eucalypts: Volume 3 Northern Australia. Inkata Press, Sydney.

Campbell, G.S. (1986) An introduction to environmental biophysics. Springer-Verlag, Berlin.

Cunningham, S.A., Summerhayes, B. & Westoby, M. (1999) Evolutionary divergences in leaf structure and chemistry, comparing rainfall and soil nutrient gradients. Ecological Monographs 69, 569-588.

Eamus, D., Myers, B., Duff, G. & Williams, R. (1999) Seasonal changes in photosynthesis of eight savanna tree species. Tree Physiology 19, 665-671.

Eamus, D., Myers, B., Duff, G. & Williams, R. (1999) A cost-benefit analysis of leaves of eight Australian savanna tree species of differing leaf life-span. Photosynthetica 36, 575-586.

Evans, J.R. (1989) Photosynthesis and nitrogen relationships in leaves of C_3 plants. Oecologia 78, 9-19.

Farquhar, G.D., O'Leary, M.H. & Berry, J.A. (1982) On the relationship between carbon isotope discrimination and the intercellular carbon dioxide concentration in leaves. Australian Journal of Plant Physiology 9, 121-137.

Farquhar, G.D. & Richards, R.A. (1984) Isotopic composition of plant carbon correlates with water-use efficiency of wheat genotypes. Australian Journal of Plant Physiology 11, 539-552.

Field, C.B. (1991) Ecological scaling of carbon gain to stress and resource availability. In: Response of Plants to Multiple Stresses (H. A. Mooney, W. E. Winner and E. J. Pell), 35-65. Academic Press, San Diego.

Hatton, T., Reece, P., Taylor, P. & McEwan, K. (1998) Does leaf water efficiency vary among eucalypts in water-limited environments? Tree Physiology 18, 529-536.

Miller, J.M., Williams, R.J. & Farquhar, G.D. (2001) Carbon isotope discrimination by a sequence of *Eucalyptus* species along a subcontinental rainfall gradient in Australia. Functional Ecology 15, 222-232.

Mooney, H.A., Ferrar, P.J. & Slatyer, R.O. (1978) Photosynthetic capacity and carbon allocation patterns in diverse growth forms of *Eucalyptus*. Oecologia 36, 103-111.

Pearcy, R.W., Björkman, O., Caldwell, M.M., Keeley, J.E., Monson, R.K. & Strain, B.R. (1987) Carbon gain by plants in natural environments. BioScience 37, 21-29.

Poorter, H. (1994) Construction costs and payback time of biomass: A whole plant perspective. In: A whole plant perspective on carbon- nitrogen interactions (J. Roy and E. Garnier), 111-127. SPB Academic Publishing, The Hague.

Reich, P.B., Ellsworth, D.S. & Walters, M.B. (1998) Leaf structure (specific leaf area) modulates photosynthesis-nitrogen relations: evidence from within and across species and functional groups. Functional Ecology 12, 948-958.

Richards, R.A. & Condon, A.G. (1993) Challenges ahead in using carbon isotope discrimination in plant-breeding programs. In: Stable Isotopes and Plant Carbon - Water Relations (J. R. Ehleringer, A. E. Hall and G. D. Farquhar), 451-462. Academic Press,, San Diego.

Roderick, M.L., Berry, S.L. & Noble, I.R. (1999c) On the relationship between leaf composition and morphoogy at elevated CO_2. New Phytologist 143, 63-72.

Roderick, M.L., Berry, S.L., Noble, I.R. & Farquhar, G.D. (1999a) A theoretical approach to linking the composition and morphology with the function of leaves. Functional Ecology 13, 683-695.

Roderick, M.L., Berry, S.L., Saunders, A.R. & Noble, I.R. (1999b) On the relationship between the composition, morphology and function of leaves. Functional Ecology 13, 696-710.

Wong, S.C., Cowan, I.R. & Farquhar, G.D. (1979) Stomatal conductance correlates with photosynthetic capacity. Nature 282, 424-426.

5.6 Tables and Figures

Figure 5.1

Leaf Δ by the 13 sampled *Eucalyptus* species in relation to the predicted mean annual rainfall at the sampling locations. In this and subsequent figures the lines show the linear regressions where there were significant trends ($\alpha = 0.05$).

Figure 5.2

Specific leaf area of the leaves used for chemical and isotopic analysis in relation to the mean annual rainfall at the sampling locations.

Figure 5.3

The mass-based leaf nitrogen concentrations of the leaves used for isotopic analysis in relation to the mean annual rainfall at the sampling locations.

Figure 5.4

The calculated mass-based net photosynthetic capacities in relation to the mean annual rainfall at the sampling locations.

Figure 5.5

The calculated area-based net photosynthetic capacities of the 13 sampled species in relation to the mean annual rainfall at the sampling locations.

Figure 5.6

The calculated intercellular CO_2 concentrations within the leaves, based on the leaf Δ values, in relation to the mean annual rainfall at the sampling locations.

Figure 5.7

The calculated leaf conductances in relation to the mean annual rainfall at the sampling locations.

Figure 5.8

The calculated transpiration values in relation to the mean annual rainfall at the sampling locations.

Figure 5.9

The calculated instantaneous water-use efficiency values in relation to the mean annual rainfall at the sampling locations.

Figure 5.10

The calculated time required for the assimilation rate to produce the carbon content in the leaves in relation to the mean annual rainfall at the sampling locations.

Figure 5.11

The potential maximum leaf area indices based on the mean annual rainfall and transpiration rates for the 13 sampled species across their distributions along the rainfall gradient.

Figure 5.12

The relationships between the predicted responses of the 13 sampled species across their distributions along the rainfall gradient.

Figure 5.13

The responses of the measured and predicted zone-mean values to decreasing total annual rainfall. Where there were significant trends, either the linear relationships (*g*, payback period, and LAI), second-order polynomials (SLA, A_{mass}, and A_{area}), or third-order polynomials (leaf Δ, *E*, and *A*/*E*) are shown.

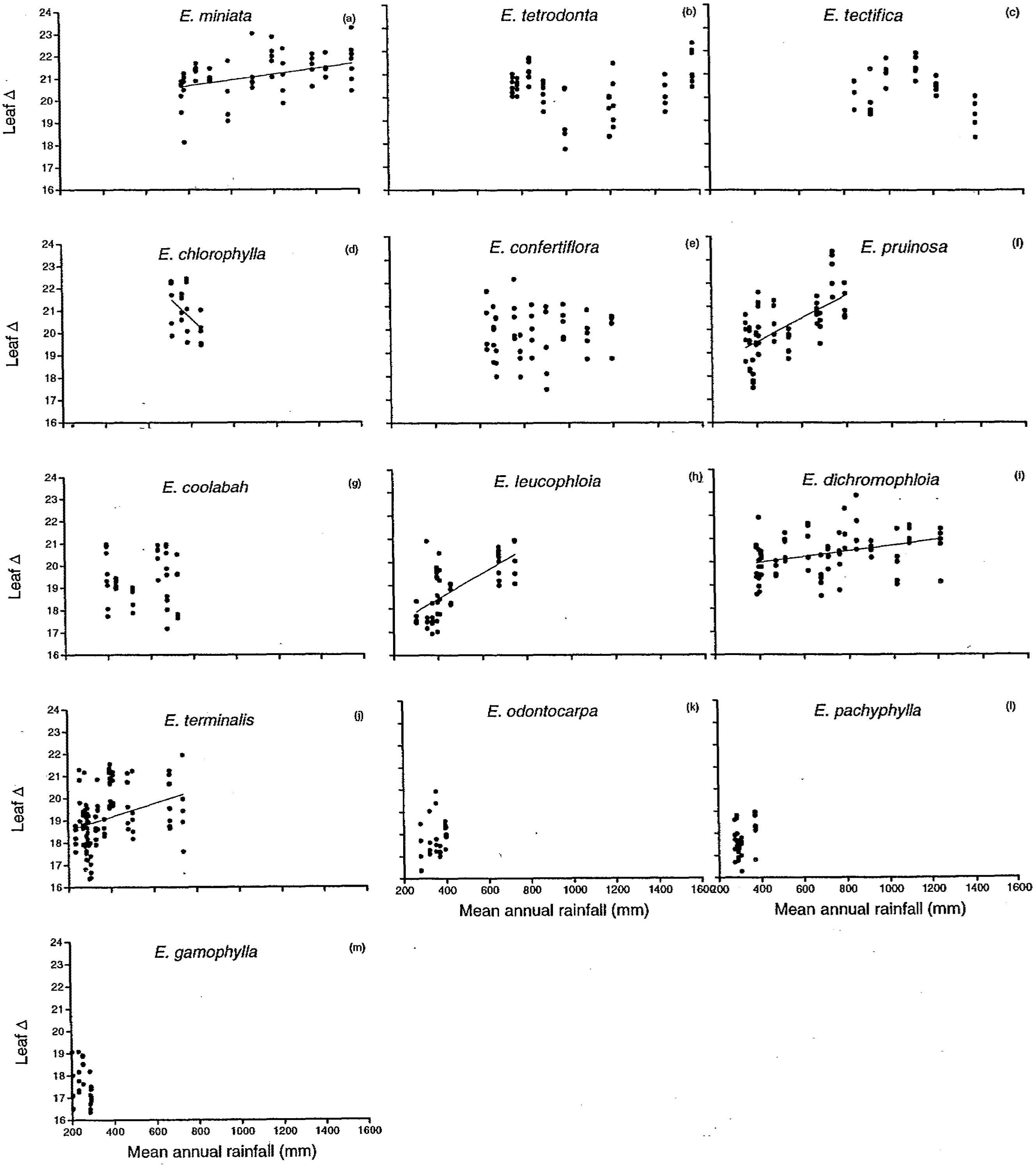

E. miniata
(a)
E. tetrodonta
(b)
E. tectifica
(c)
E. chlorophylla
(d)
E. confertiflora
(e)
E. pruinosa
(f)
E. coolabah
(g)
E. leucophloia
(h)
E. dichromophloia
(i)
E. terminalis
(j)
E. odontocarpa
(k)
E. pachyphylla
(l)
E. gamophylla
(m)
Leaf Δ
24
23
22
21
20
19
18
17
16
200
400
600
800
1000
1200
1400
1600
Mean annual rainfall (mm)

Figure 5.1

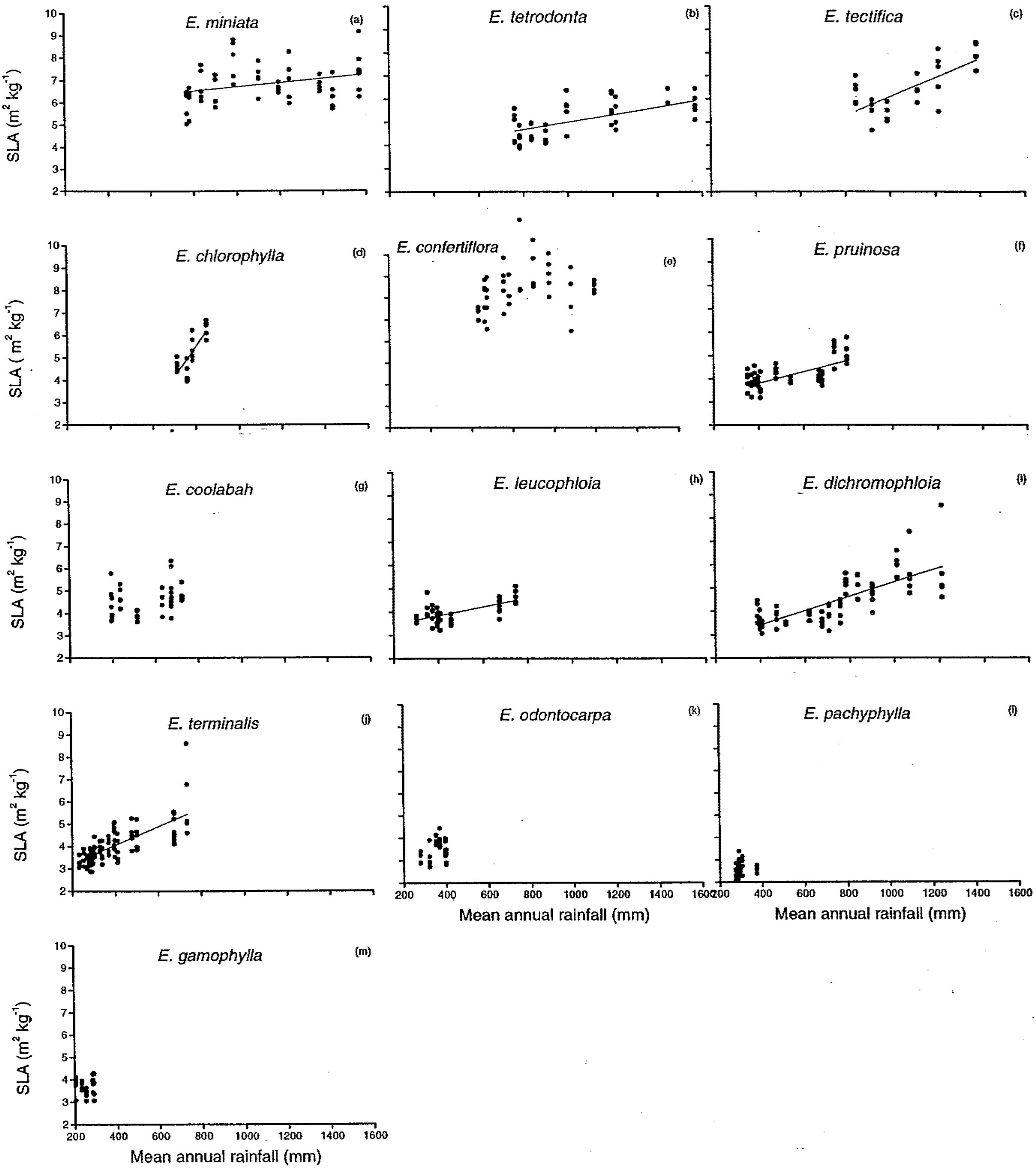

E. miniata
(a)
E. tetrodonta
(b)
E. tectifica
(c)
E. chlorophylla
(d)
E. confertiflora
(e)
E. pruinosa
(f)
E. coolabah
(g)
E. leucophloia
(h)
E. dichromophloia
(i)
E. terminalis
(j)
E. odontocarpa
(k)
E. pachyphylla
(l)
E. gamophylla
(m)
SLA (m^2 kg^{-1})
2
3
4
5
6
7
8
9
10
200
400
600
800
1000
1200
1400
1600
Mean annual rainfall (mm)

Figure 5.2

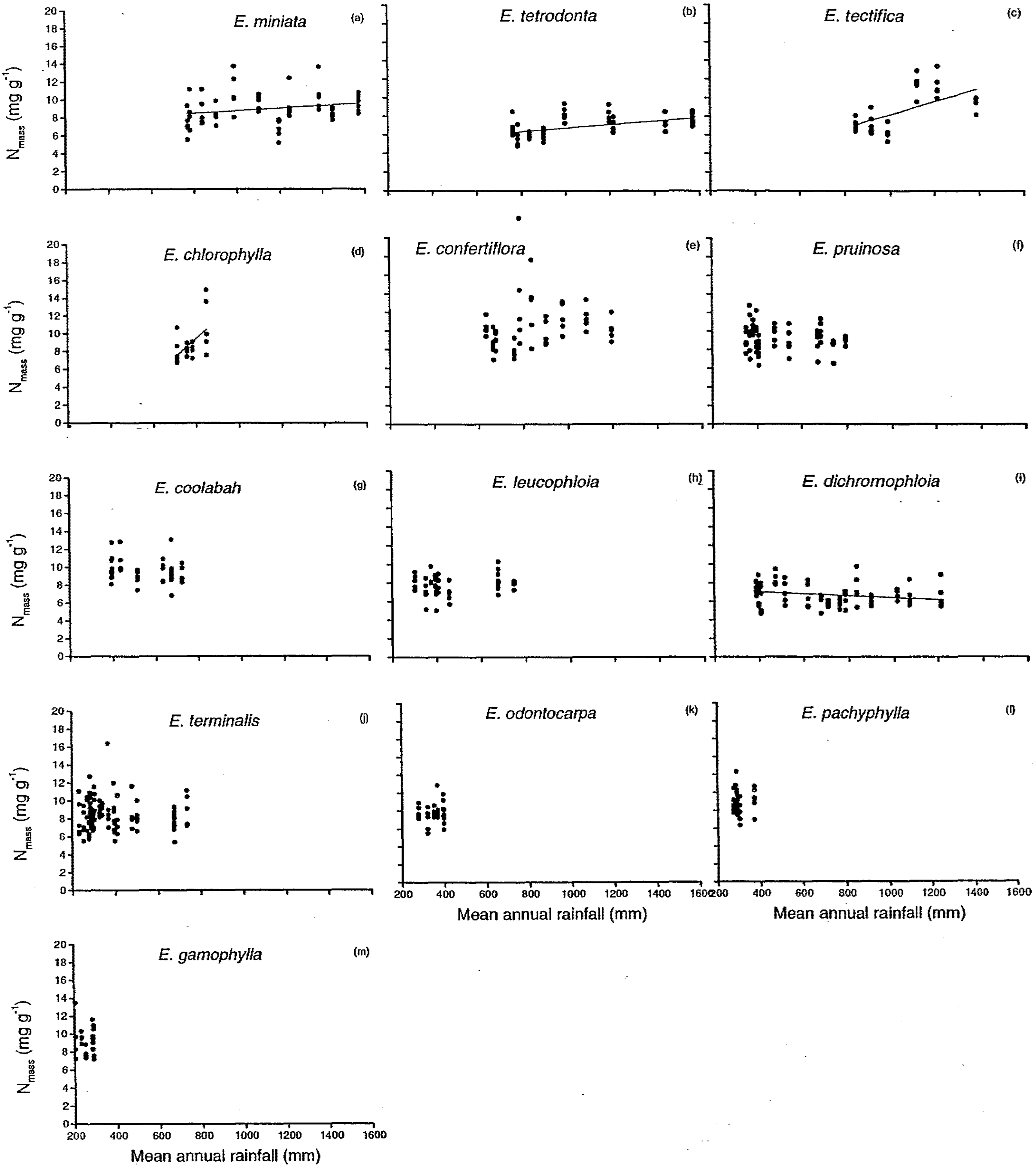

E. miniata
(a)
E. tetrodonta
(b)
E. tectifica
(c)
E. chlorophylla
(d)
E. confertiflora
(e)
E. pruinosa
(f)
E. coolabah
(g)
E. leucophloia
(h)
E. dichromophloia
(i)
E. terminalis
(j)
E. odontocarpa
(k)
E. pachyphylla
(l)
E. gamophylla
(m)
N_{mass} (mg g^{-1})
0
2
4
6
8
10
12
14
16
18
20
200
400
600
800
1000
1200
1400
1600
Mean annual rainfall (mm)

Figure 5.3

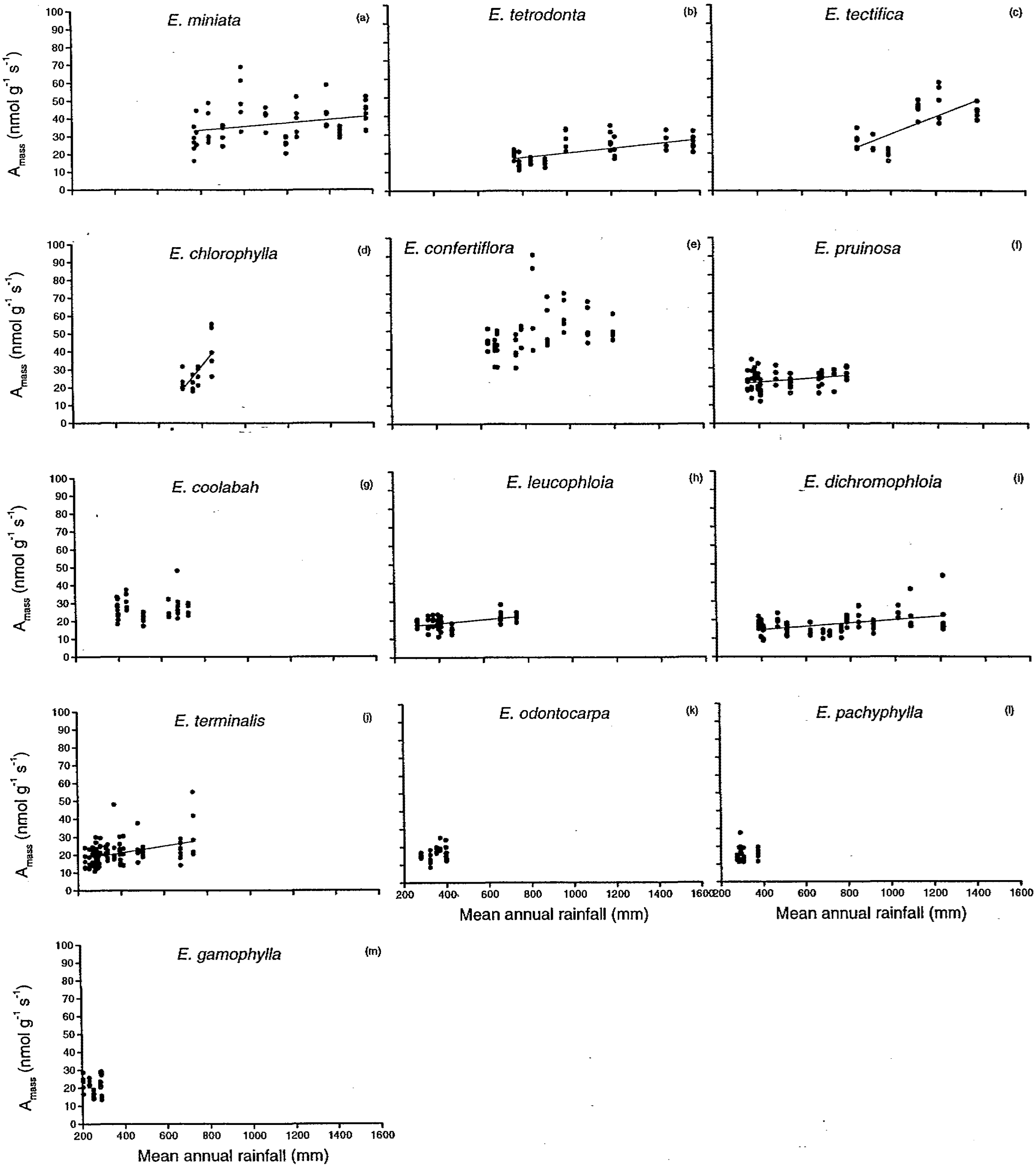

E. miniata (a)
E. tetrodonta (b)
E. tectifica (c)
E. chlorophylla (d)
E. confertiflora (e)
E. pruinosa (f)
E. coolabah (g)
E. leucophloia (h)
E. dichromophloia (i)
E. terminalis (j)
E. odontocarpa (k)
E. pachyphylla (l)
E. gamophylla (m)
A_{mass} (nmol g^{-1} s^{-1})
0
10
20
30
40
50
60
70
80
90
100
200
400
600
800
1000
1200
1400
1600
Mean annual rainfall (mm)

Figure 5.4

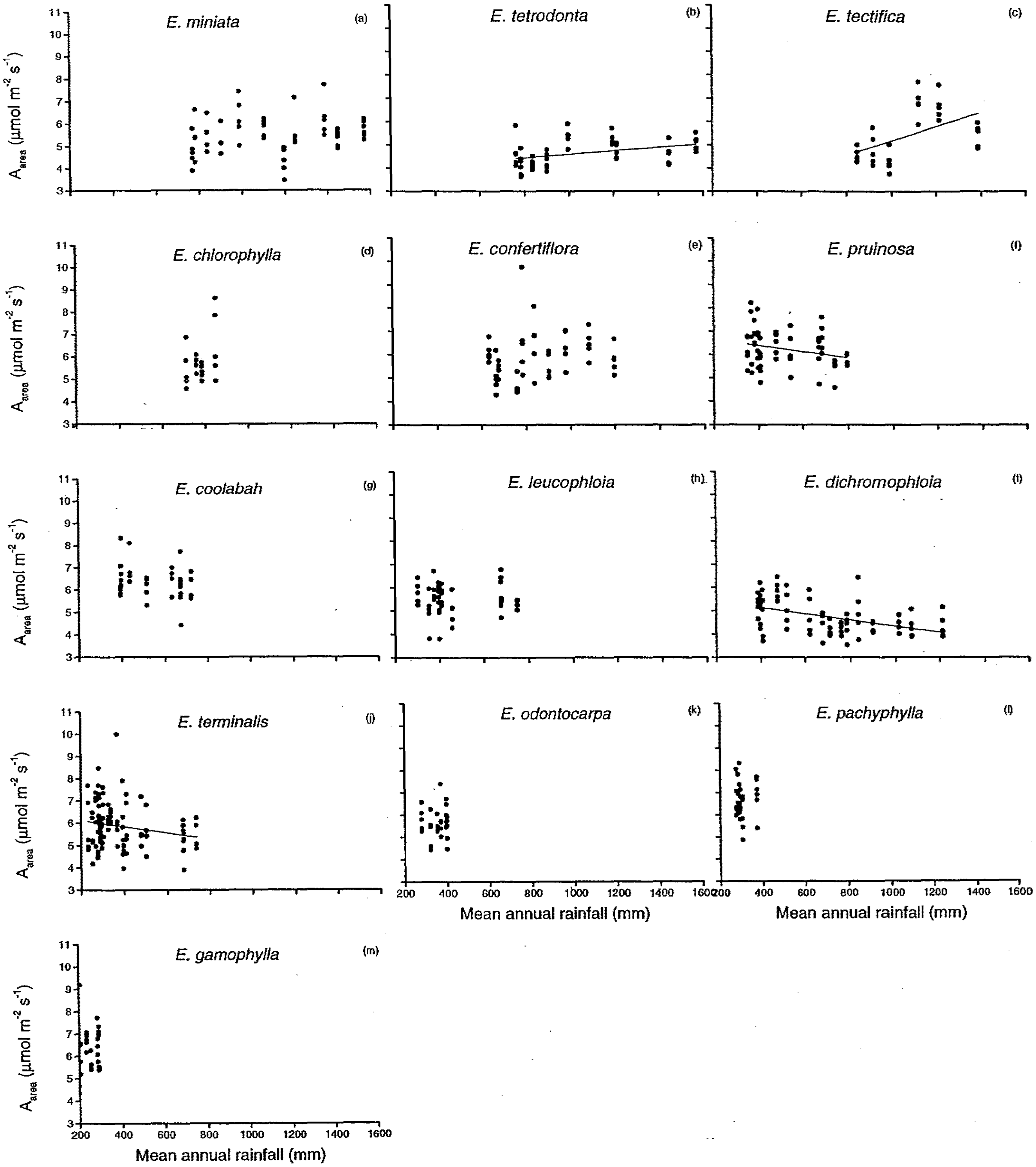

E. miniata
(a)
E. tetrodonta
(b)
E. tectifica
(c)
E. chlorophylla
(d)
E. confertiflora
(e)
E. pruinosa
(f)
E. coolabah
(g)
E. leucophloia
(h)
E. dichromophloia
(i)
E. terminalis
(j)
E. odontocarpa
(k)
E. pachyphylla
(l)
E. gamophylla
(m)
A_area (µmol m^-2 s^-1)
3
4
5
6
7
8
9
10
11
200
400
600
800
1000
1200
1400
1600
Mean annual rainfall (mm)

Figure 5.5

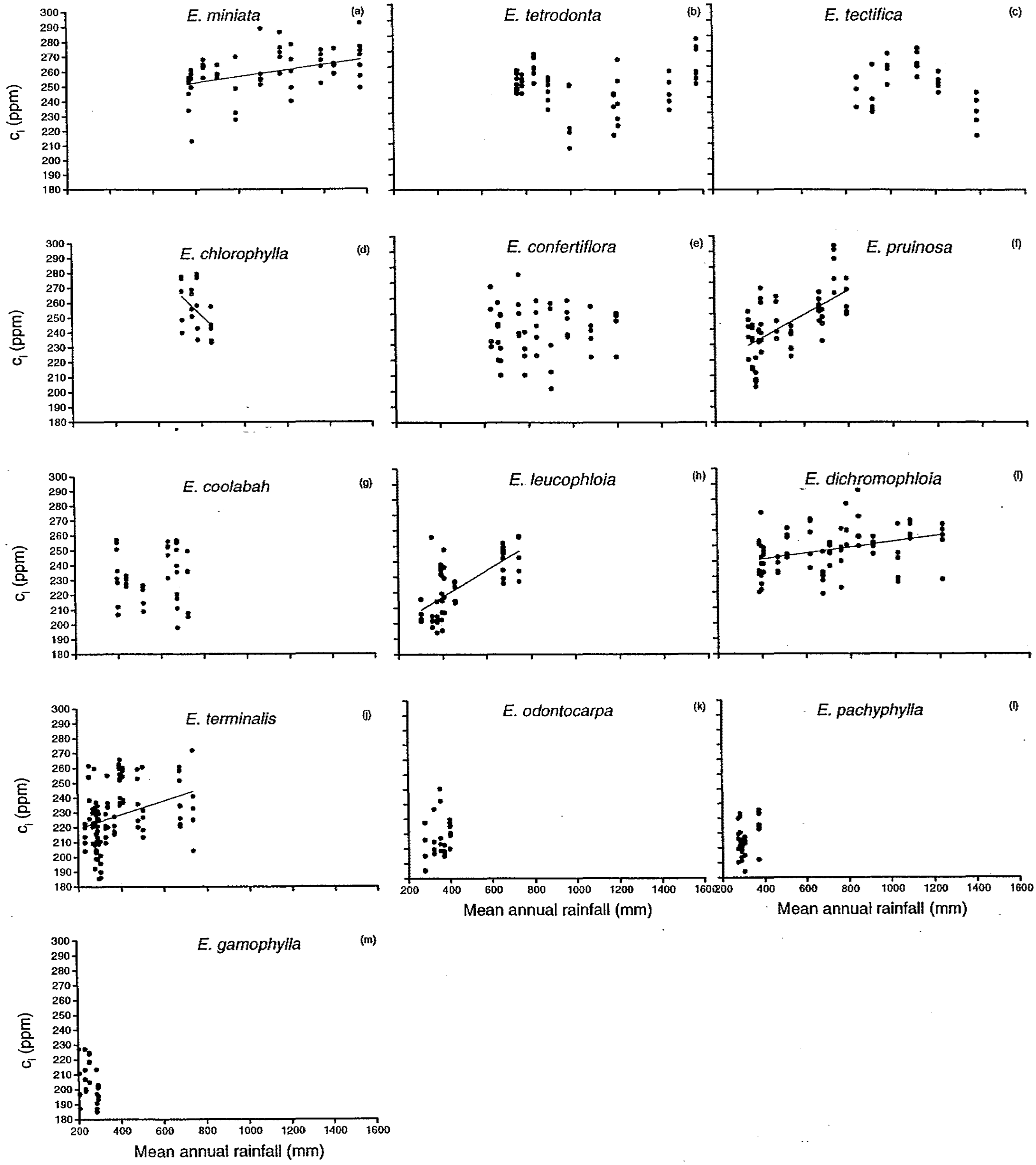

E. miniata
(a)
E. tetrodonta
(b)
E. tectifica
(c)
E. chlorophylla
(d)
E. confertiflora
(e)
E. pruinosa
(f)
E. coolabah
(g)
E. leucophloia
(h)
E. dichromophloia
(i)
E. terminalis
(j)
E. odontocarpa
(k)
E. pachyphylla
(l)
E. gamophylla
(m)
c_i (ppm)
300
290
280
270
260
250
240
230
220
210
200
190
180
200
400
600
800
1000
1200
1400
1600
Mean annual rainfall (mm)

Figure 5.6

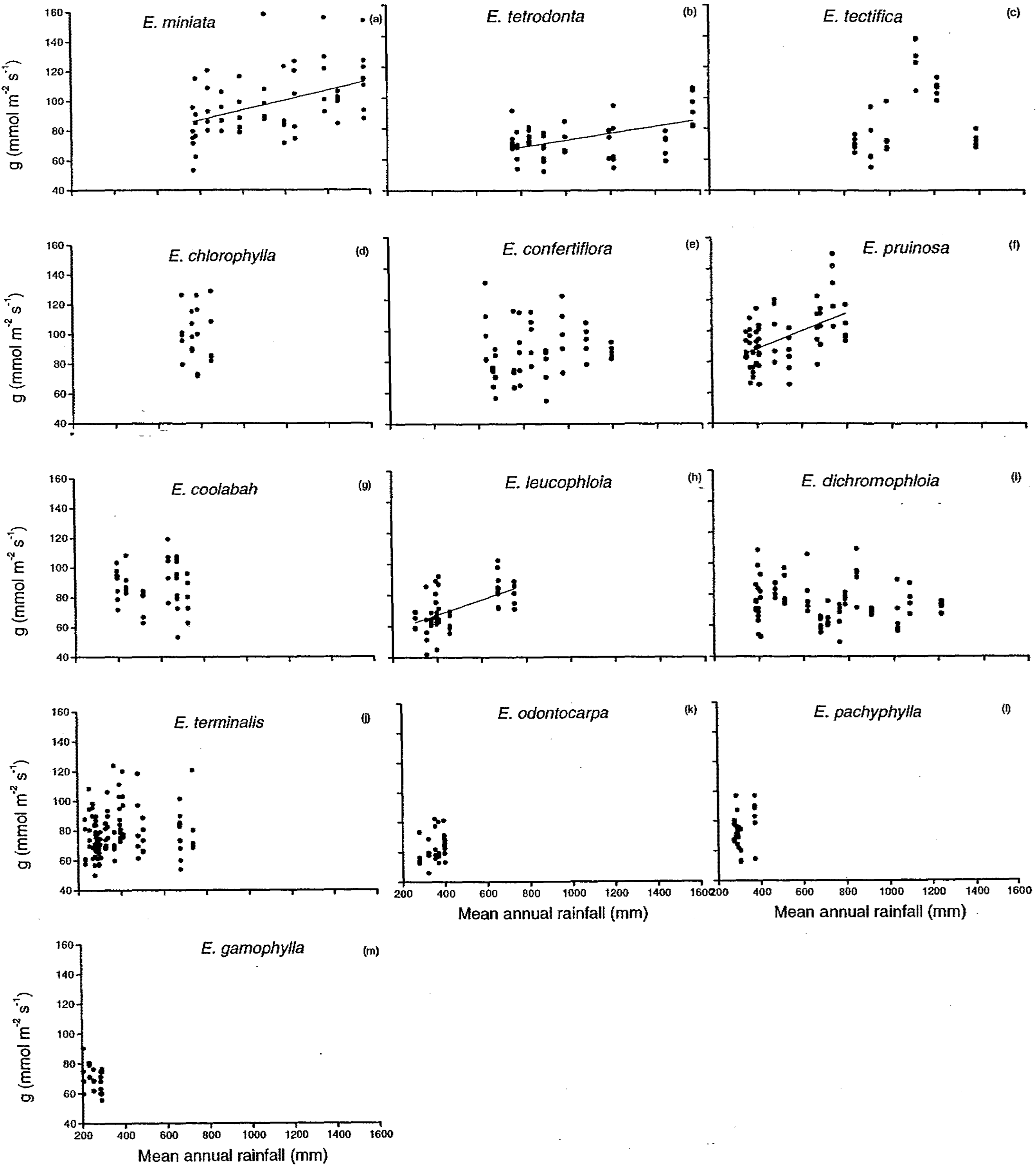

E. miniata
(a)
E. tetrodonta
(b)
E. tectifica
(c)
E. chlorophylla
(d)
E. confertiflora
(e)
E. pruinosa
(f)
E. coolabah
(g)
E. leucophloia
(h)
E. dichromophloia
(i)
E. terminalis
(j)
E. odontocarpa
(k)
E. pachyphylla
(l)
E. gamophylla
(m)
g (mmol m^{-2} s^{-1})
160
140
120
100
80
60
40
200
400
600
800
1000
1200
1400
1600
Mean annual rainfall (mm)

Figure 5.7

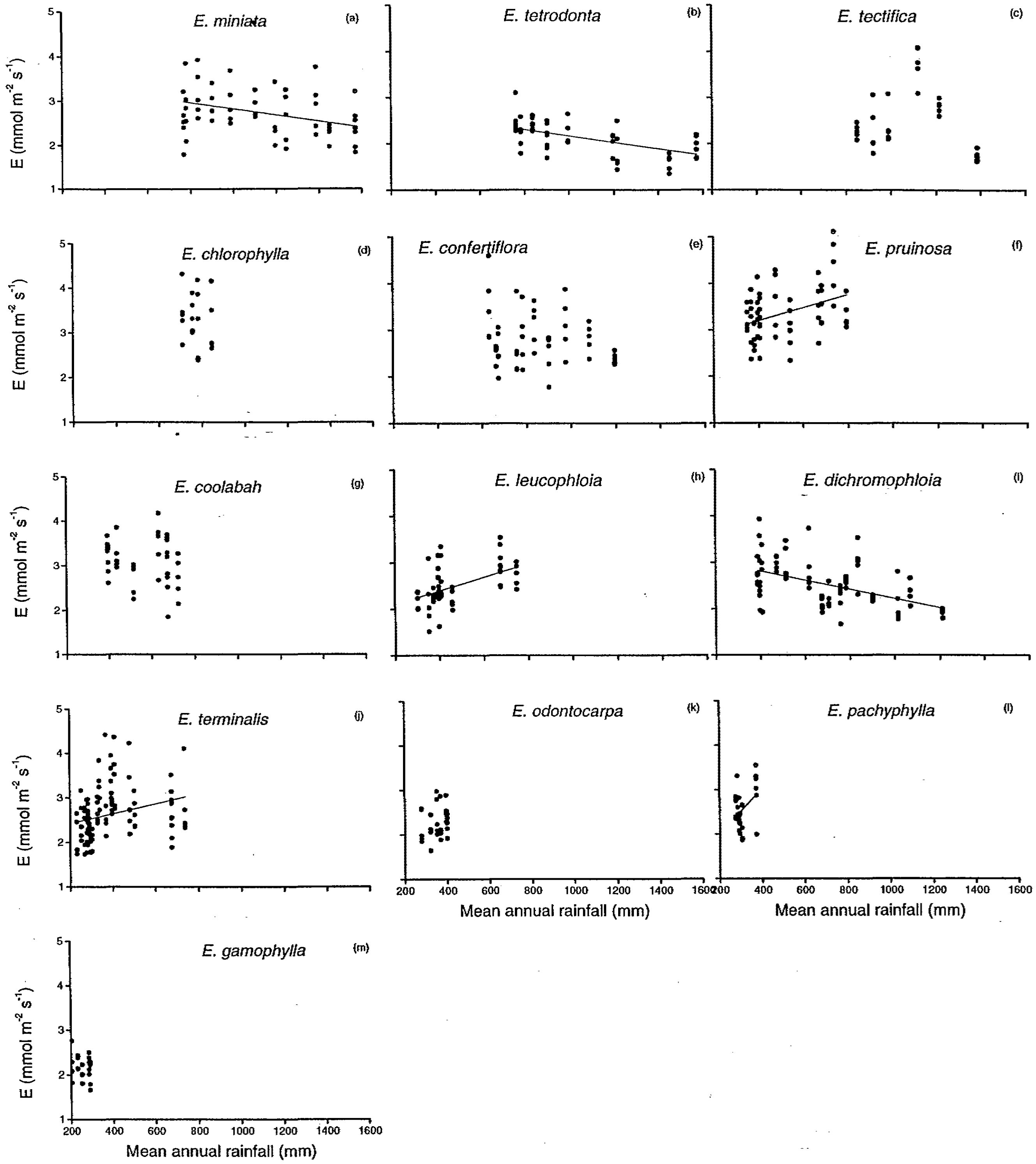

E. miniata (a)
E. tetrodonta (b)
E. tectifica (c)
E. chlorophylla (d)
E. confertiflora (e)
E. pruinosa (f)
E. coolabah (g)
E. leucophloia (h)
E. dichromophloia (i)
E. terminalis (j)
E. odontocarpa (k)
E. pachyphylla (l)
E. gamophylla (m)
E (mmol m-2 s-1)
1
2
3
4
5
200
400
600
800
1000
1200
1400
1600
Mean annual rainfall (mm)

Figure 5.8

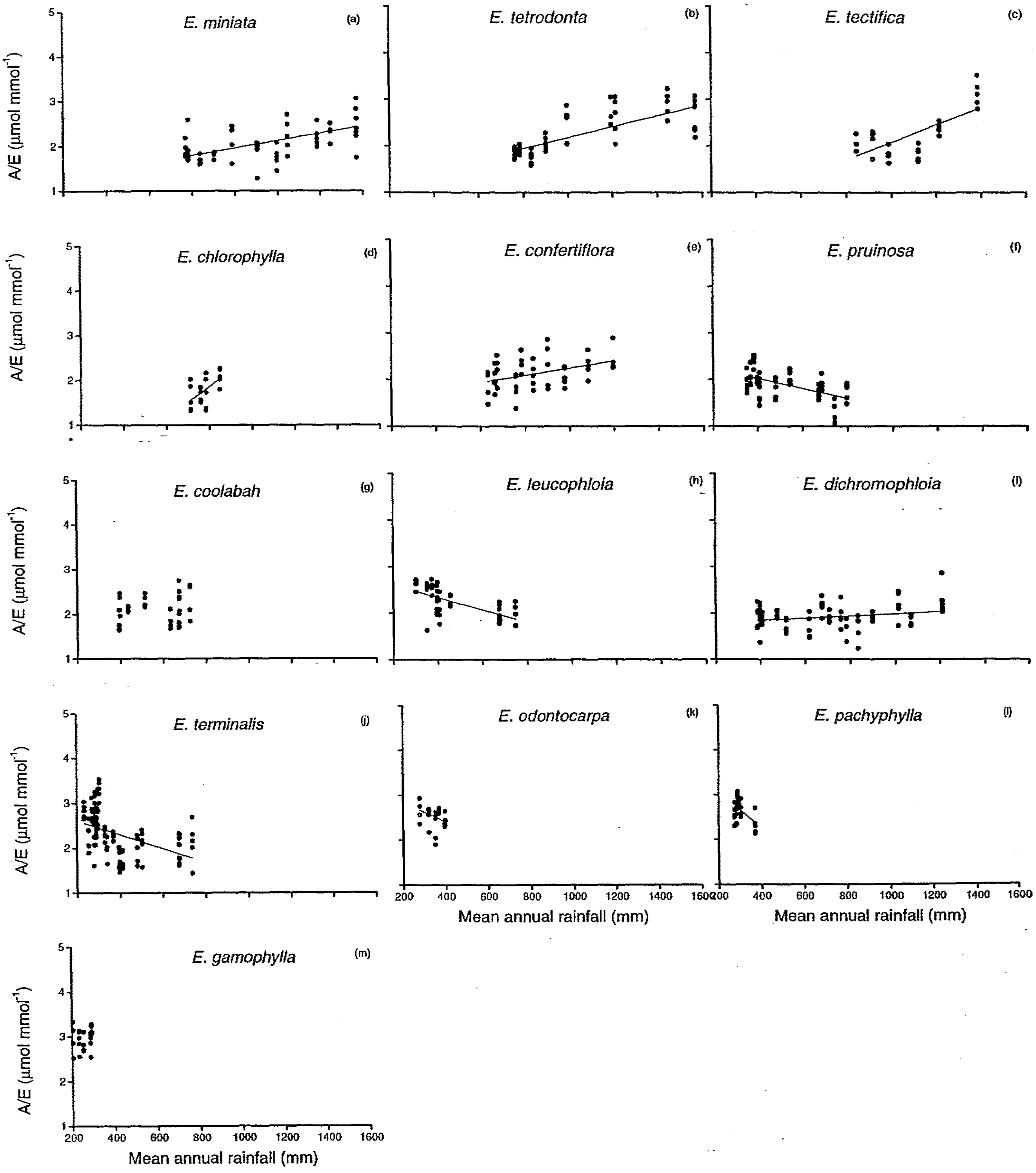

E. miniata (a)
E. tetrodonta (b)
E. tectifica (c)
E. chlorophylla (d)
E. confertiflora (e)
E. pruinosa (f)
E. coolabah (g)
E. leucophloia (h)
E. dichromophloia (i)
E. terminalis (j)
E. odontocarpa (k)
E. pachyphylla (l)
E. gamophylla (m)
A/E (μmol mmol-1)
1
2
3
4
5
200
400
600
800
1000
1200
1400
1600
Mean annual rainfall (mm)

Figure 5.9

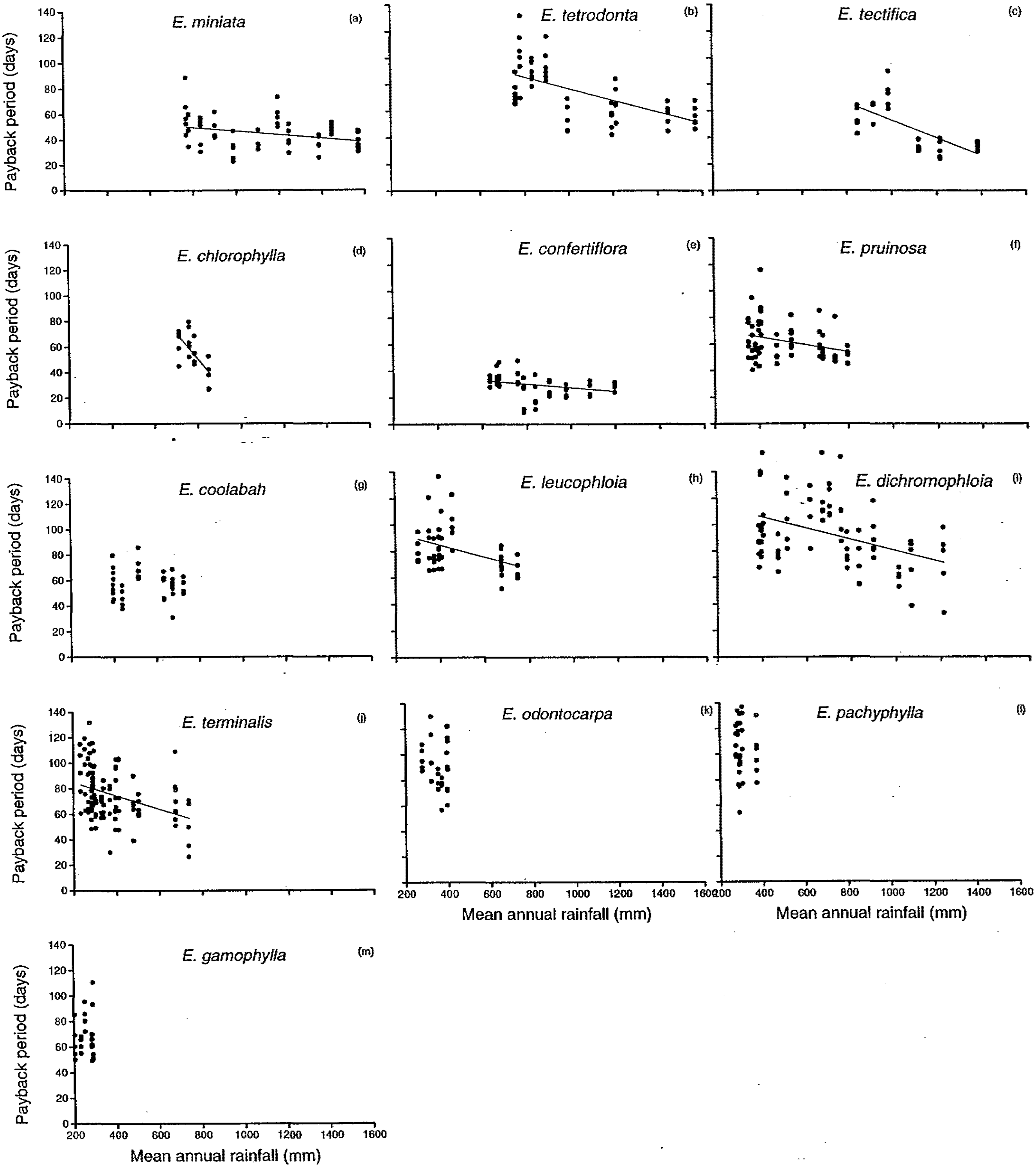

Payback period (days)
0
20
40
60
80
100
120
140
E. miniata
(a)
E. tetrodonta
(b)
E. tectifica
(c)
E. chlorophylla
(d)
E. confertiflora
(e)
E. pruinosa
(f)
E. coolabah
(g)
E. leucophloia
(h)
E. dichromophloia
(i)
E. terminalis
(j)
E. odontocarpa
(k)
E. pachyphylla
(l)
E. gamophylla
(m)
200
400
600
800
1000
1200
1400
1600
Mean annual rainfall (mm)

Figure 5.10

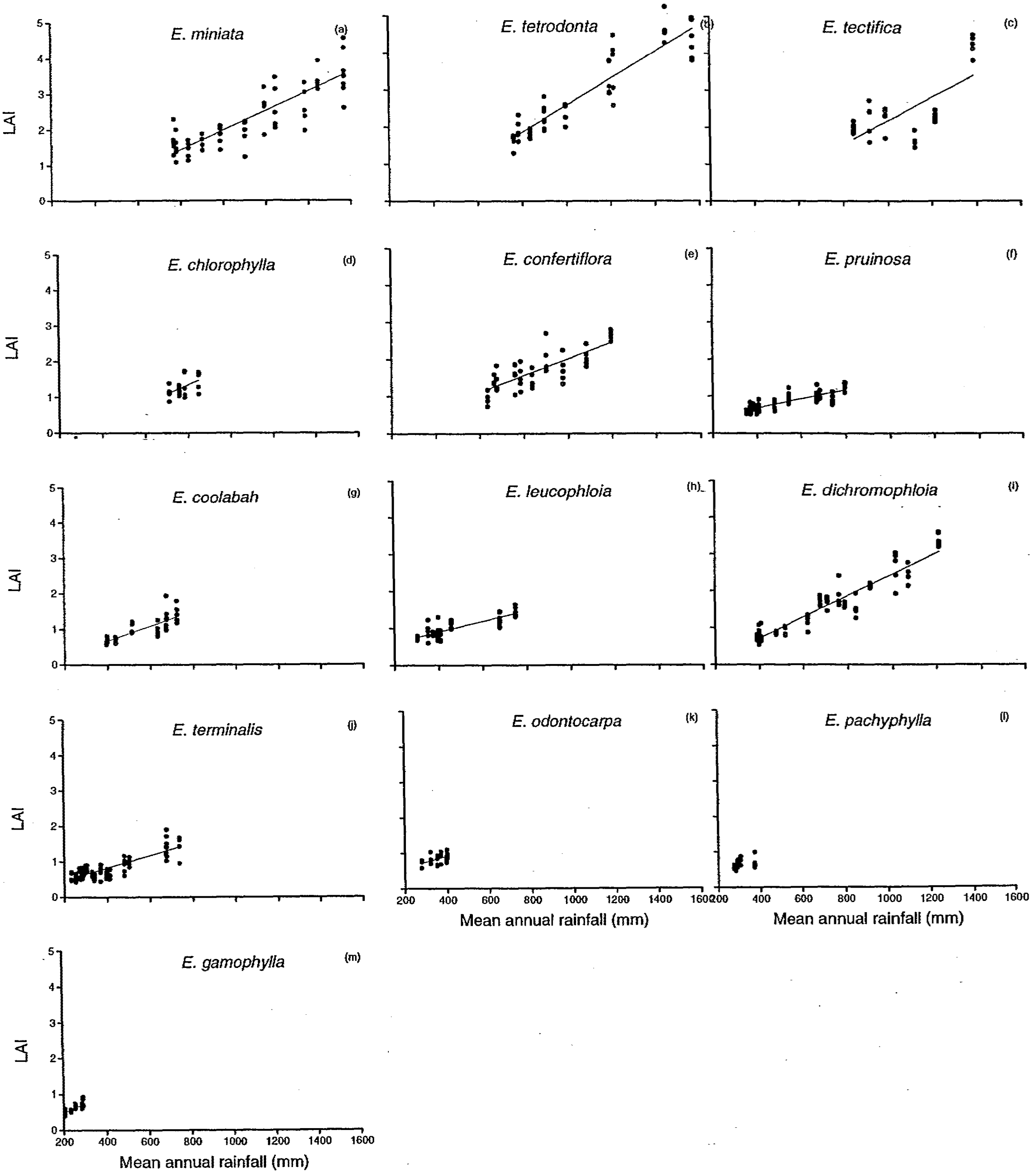

E. miniata
(a)
E. tetrodonta
(b)
E. tectifica
(c)
E. chlorophylla
(d)
E. confertiflora
(e)
E. pruinosa
(f)
E. coolabah
(g)
E. leucophloia
(h)
E. dichromophloia
(i)
E. terminalis
(j)
E. odontocarpa
(k)
E. pachyphylla
(l)
E. gamophylla
(m)
LAI
0
1
2
3
4
5
200
400
600
800
1000
1200
1400
1600
Mean annual rainfall (mm)

Figure 5.11

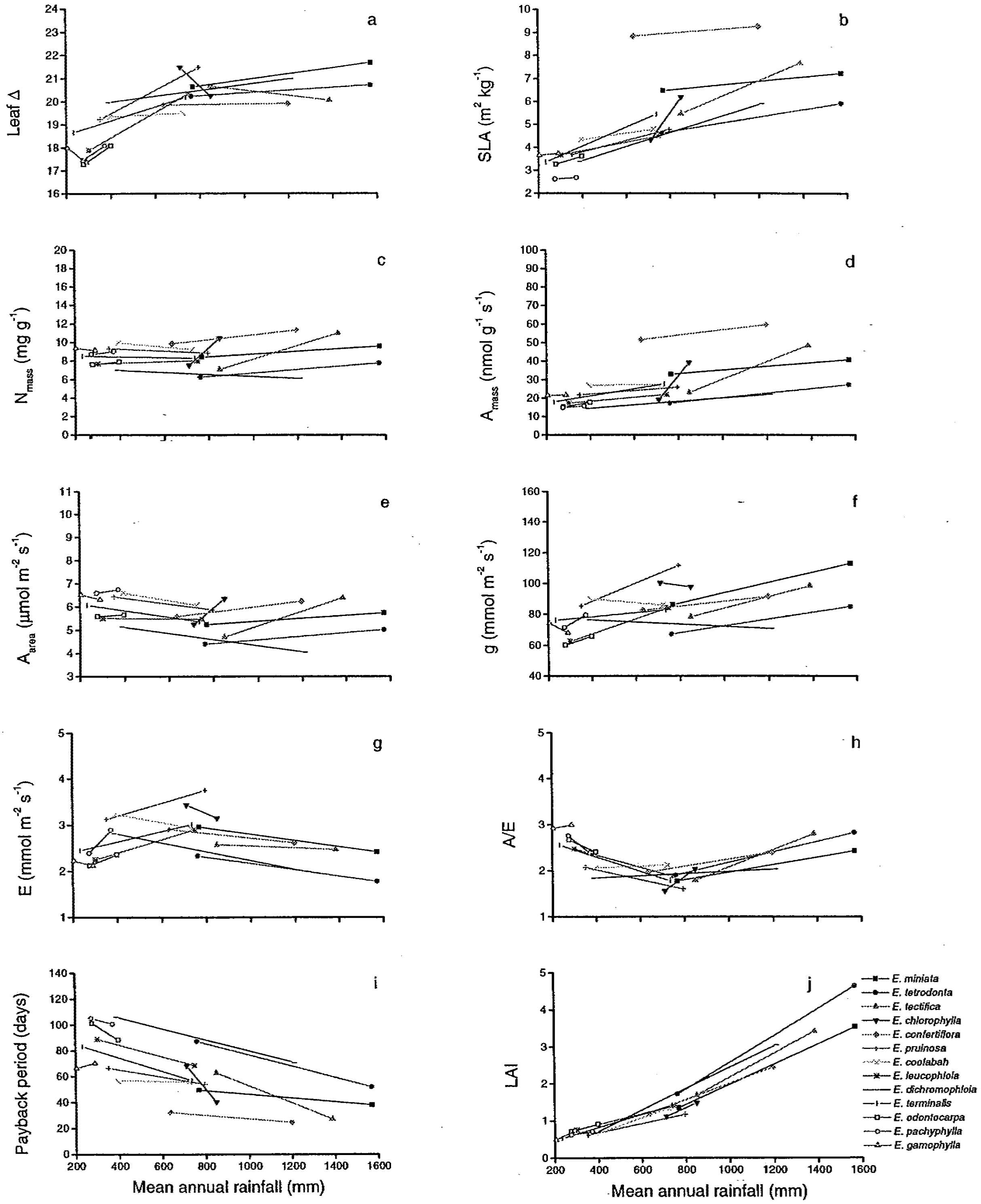
a
Leaf Δ
b
SLA ($m^2 kg^{-1}$)
c
N_{mass} ($mg g^{-1}$)
d
A_{mass} ($nmol g^{-1} s^{-1}$)
e
A_{area} ($\mu mol m^{-2} s^{-1}$)
f
g ($mmol m^{-2} s^{-1}$)
g
E ($mmol m^{-2} s^{-1}$)
h
A/E
i
Payback period (days)
j
LAI
200 400 600 800 1000 1200 1400 1600
Mean annual rainfall (mm)
E. miniata
E. tetrodonta
E. tectifica
E. chlorophylla
E. confertiflora
E. pruinosa
E. coolabah
E. leucophloia
E. dichromophloia
E. terminalis
E. odontocarpa
E. pachyphylla
E. gamophylla

Figure 5.12

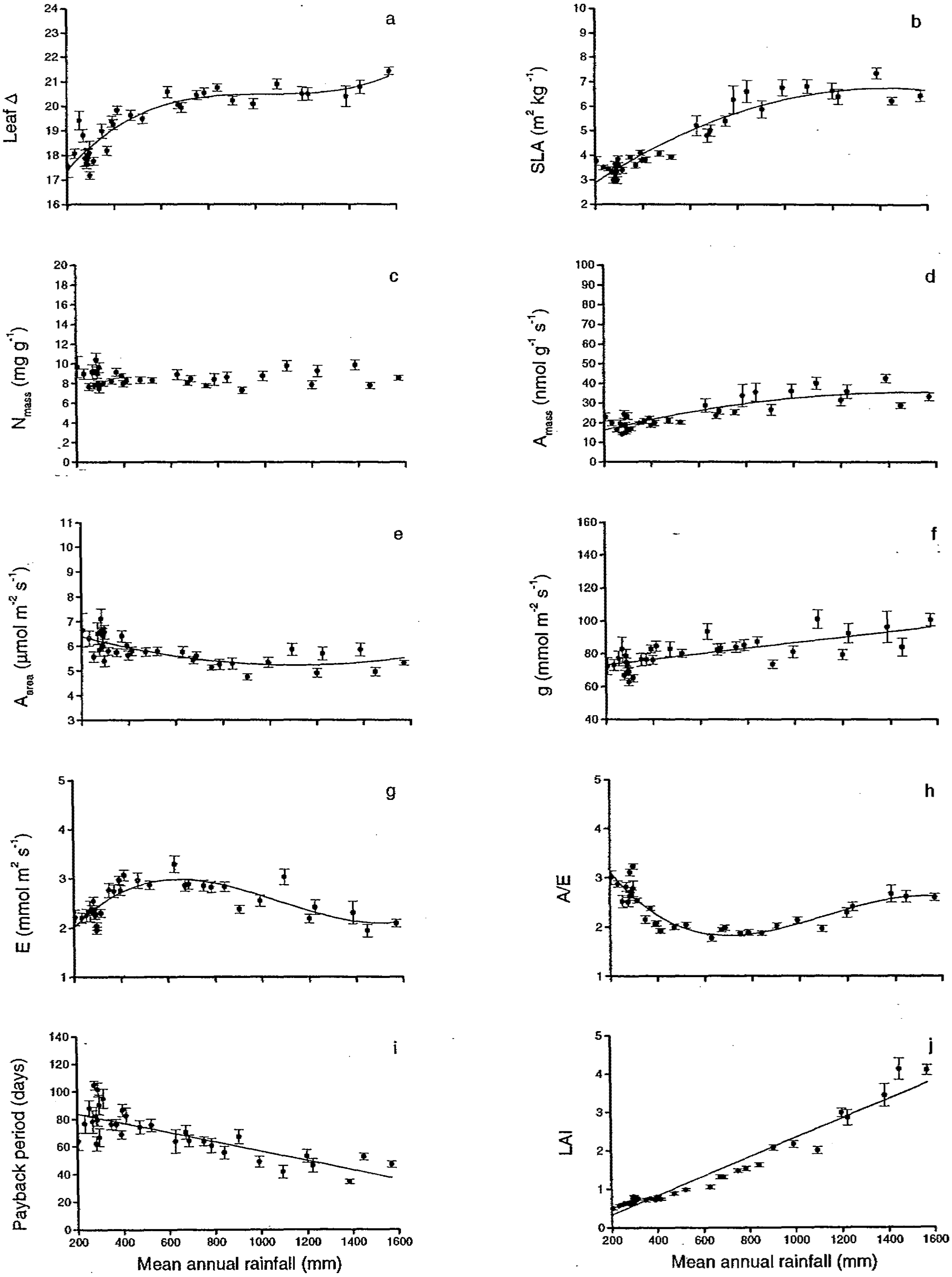
a
Leaf Δ
16
17
18
19
20
21
22
23
24
b
SLA (m^2 kg^{-1})
2
3
4
5
6
7
8
9
10
c
N_{mass} (mg g^{-1})
0
2
4
6
8
10
12
14
16
18
20
d
A_{mass} (nmol g^{-1} s^{-1})
0
10
20
30
40
50
60
70
80
90
100
e
A_{area} (μmol m^{-2} s^{-1})
3
4
5
6
7
8
9
10
11
f
g (mmol m^{-2} s^{-1})
40
60
80
100
120
140
160
g
E (mmol m^{2} s^{-1})
1
2
3
4
5
h
A/E
1
2
3
4
5
i
Payback period (days)
0
20
40
60
80
100
120
140
200
400
600
800
1000
1200
1400
1600
Mean annual rainfall (mm)
j
LAI
0
1
2
3
4
5
200
400
600
800
1000
1200
1400
1600
Mean annual rainfall (mm)

Figure 5.13

Chapter 6

Environmental correlates of leaf and wood carbon isotope discrimination at the species and functional type levels in Australian *Eucalyptus* species

Summary

1. Carbon isotope discrimination reflects the balance between leaf conductance and photosynthetic CO_2 uptake. Variation in Δ can arise from variation in either g or A. Patterns in Δ resulting from variation in g could be interpreted as measures of stomatal limitation on photosynthesis, with low Δ reflecting low carbon gain and decreased plant fitness. Decreases in Δ resulting from increases in A could be interpreted as measures of increased carbon gain, water-use efficiency, and plant fitness.

2. Across an 8-fold gradient of decreasing rainfall in the Northern Territory of Australia the leaf and wood Δ were correlated with photosynthetic capacities calculated from leaf nitrogen contents and a calculated estimate of long-term average leaf conductances.

3. Carbon isotope discrimination showed stronger correlations with the calculated g estimate than with the calculated A estimate.

4. Carbon isotope discrimination also exhibited higher correlations with factors affecting plant water relations than with leaf nitrogen concentrations. These factors included rainfall amounts, the time intervals between rainfall events, and the evaporative demand.

6.1 Introduction

The carbon isotope discrimination (Δ) recorded in leaf and wood tissue is thought to record the balance between the supply of CO_2 into, and demand from, the intercellular air spaces of the leaves during the initial steps of photosynthesis (Farquhar, O'Leary & Berry 1982). The relationship between the photosynthetic CO_2 assimilation rate (A), the leaf conductance to water vapour (g), and Δ can be described by

$$\Delta = a + (b - a)\left(1 - \frac{AP}{g\,p_a}\right) \qquad \text{(Eq. 6.1)}$$

where a is the discrimination against ^{13}C during diffusion through the stomata, b is the discrimination against ^{13}C by Rubisco, p_a is the ambient CO_2 partial pressure, and P is the total atmospheric pressure following the model of Farquhar *et al.* (1982).

Variation in Δ can arise from either variation in A with a constant g, variation in g with a constant A, or variation in both A and g in opposite directions (Ehleringer & Cook 1990; Virgona & Farquhar 1996). Synchronous movement of both A and g in the same direction could result in little change in Δ, while still having significant effects on plant performance. In naturally occurring plant populations along a gradient of decreasing water availability, patterns of decreasing Δ resulting from decreasing g and constant A could be interpreted as a measure of increasing stomatal limitation on assimilation and decreasing plant fitness. Patterns of decreasing Δ resulting from increasing A and constant g would reflect patterns of increased leaf N investment, i.e. resource substitution, and possibly increased plant fitness. The increased carbon gain per unit leaf area and higher water-use efficiency would have to be offset by a decreasing leaf-area index if transpiration was to remain unchanged while water supply decreased.

Directly measuring long-term average assimilation rates of around 650 individual trees over a 1750km transect would not be easy. Assimilation capacity, predicted from leaf nitrogen contents and specific leaf area (Reich, Ellsworth & Walters 1998), provides a long-term measure of potential assimilation rates with the appropriate time-scale. Unfortunately, actual assimilation rates will probably always be lower than the potential rates, and in many cases may exhibit little correlation. Leaf conductances, calculated from the potential assimilation rate and leaf Δ do not provide an independent measure of that important parameter. Although it would have been ideal to have been able to rigorously test the importance of A versus g in determining the patterns in Δ, in this exercise it should be remembered that any correlation presented with g is actually a correlation with A/Δ. In naturally occurring, rain-fed trees that have not undergone a graduated fertilizer treatment, Δ values should show stronger correlations with g than with A, if for no other reason than the environmental events that affect g happen with a higher frequency than those which affect A and there will therefore be more variation in g than in A within an individual during any time period.

Given that the estimates of A and g are not the most robust, the correlations of leaf and wood Δ with the environmental and morphological parameters which might affect A and g may yield more information than the relationships between A and g and the Δ values themselves. Carbon isotope discrimination may be correlated with leaf nitrogen contents, but not in the relationship used to determine A. Environmental parameters determining the supply and demand for water (which should influence g) may also correlate with Δ, while not with g as calculated here (see Chapter 5). Indices weighting the demand for water with its availability (Comstock & Ehleringer 1992), the hydraulic path length (Ryan & Yoder 1997), and variation in leaf chemistry may also affect Δ values (Schmidt & Gleixner 1998).

6.2 Methods

Leaf and wood samples of dominate *Eucalyptus* overstory tree species were collected along a 1750 km section of the Stuart Highway between Darwin (~ 12 ½°S) and the southern border of the Northern Territory (~ 25°S) as described in Chapter 3 and Miller, Williams & Farquhar (2001). As noted earlier, not all the species co-occurred at exactly the same location in mixed stands of multiple species. Where possible all of the species of interest were sampled where they were co-located, or were as close together as possible (Table 6.1).

The analysis methods of the samples of leaf and wood tissue for Δ, leaf mass per unit area (LMA), and leaf nitrogen and carbon contents (N_{mass}, N_{area}, C_{mass}, and C_{area}) were described in Chapters 3 and 4. When tissue was collected in the field the diameter of the trunk at breast height was recorded for each individual tree as was the height to the bottom and top of the leaf canopy.

The monthly mean climatic data were generated by ANUCLIM 1.8 (Centre for Resource and Environmental Studies, ANU) as described in Chapter 3. Photosynthetic capacities, leaf conductances, transpiration rates, and leaf payback periods were calculated as described in Chapter 5.

An index weighting evaporative demand by moisture availability (Comstock & Ehleringer 1992) was calculated as

$$\omega = {\left[\frac{1}{P}\right]\sum_{\mathrm{Jan}}^{\mathrm{Dec}} e_s \frac{W}{E_p}} \Bigg/ {\sum_{\mathrm{Jan}}^{\mathrm{Dec}} \frac{W}{E_p}} \qquad \text{(Eq. 6.2)}$$

where P is the total atmospheric pressure, e_s is the saturation vapor pressure of the air, W is the average monthly precipitation, and E_p is the potential evapotranspiration.

Statistical analyses were made using SAS (6.12: SAS Institute Inc.), SYSTAT (9.01: SPSS Inc,), and Microcal Origin 5.0. Leaf and wood Δ were correlated with a suite of biotic (Table 6.2) and environmental (Table 6.3) parameters. The possible parameters for inclusion in the step-wise regression models were the same as used in the correlation analyses, and also included the monthly mean environmental values (i.e. the monthly rainfall values, monthly saturated vapor pressure deficits and potential evaporations, monthly average solar radiation, monthly mean maximum and minimum temperatures, and the monthly number of rain days and average drought lengths).

6.3 Results

Transect climate parameters

Along the transect in this study, which covered half the latitudinal span of continental Australia, there were significant trends in most of the climatic parameters that could possibly affect plant physiological processes and limit species distributions. The climate is monsoonal, with a four month wet season receiving most of the total annual rainfall, but both the amount of rainfall and the seasonality vary across the transect. The length of the annual dry season varies, as do the intervals between rain events (drought lengths), as well as the patterns of evaporative demand in different times of the year. And finally, although mean maximum and minimum temperatures are not that variable, patterns of extreme events could be important.

The elevations along the transect (from a digital elevation map) ranged from nearly sea level in the north to approximately 700 m at about 23°S (Figure 6.1a). The area was not marked by any particularly striking topographic variations. Mean annual rainfall varied along the transect from about 1600 mm yr^{-1} in the north to about 200 mm yr^{-1} in the south (Figure 6.1b). The decrease in mean annual rainfall was not linearly related to increasing latitude, and an exponential decay function described most of the variability in the data ($r^2 = 0.99$) . Around 80% of the rain occurs during the months of December to March (hereafter referred to as the wet-season) in the northern half of the transect (north of 18½°S). As latitude increases the rainfall then becomes less seasonal, and at the southern edge of the transect only 50% of the rainfall occurs during the wet-season (Figure 6.1c). During the months of June through September (the dry-season) the areas north of approximately 16½°S receive less than 2% of the mean annual rainfall, while at the southern edge of the transect 20% of the rainfall occurs during these months. The two transition periods, April and May, and October and November account for about 20% of the mean annual rainfall in Darwin, between 16 to 18% of the mean annual rainfall between 14½°S and 19°S, and amounts increasing to about 30% in the south.

The area north of 14½°S experiences the beginning of the wet-season about a month earlier than the rest of the transect. The average interval between raindays (drought length) during the dry-season increases from around 30 to 65 days between 14 and 15°S (Figure 6.1d). The average dry-season drought length then decreases toward the south as the occurrence of dry-season rain events, although small in magnitude, increases. In the wet-season there is less than a full day between rain events on average in the north (Figure 6.1e). The wet-season average drought length increases uniformly to about 5 days at 23½°S and then up to 7 days at 25°S. The pattern of the average drought length during the transition months reflects the rain events arriving from both the north and south ends of the transect. Between 15 and 21°S there is a pattern of increasing average drought length from about 7 to 10 days, with shorter intervals further to both the north and south.

Mean maximum and mean minimum temperatures do not vary greatly across the transect (Figure 6.1f). Annual mean minimum temperatures are around 20°C north of 20°S, and then drop to around 13.5°C south of 23°S. Annual mean maximum temperatures vary between 30 and 35°C. The wet-season is the southern hemisphere summer, so the wet-season temperatures are higher than the annual means, especially in the south. The average daily incoming solar radiation increases toward the south during the wet-season, reflecting the position of the sun (Figure 6.1g). The mean annual daily solar radiation does not exhibit a trend across the transect.

The average mid-afternoon saturated vapor pressure deficits (SVPD) during the wet-season increased from the north to around 20°S, and then were relatively constant (Figure 6.1h). During the transition seasons the SVPD values increased to about 14°S, and then were relatively constant to about 21°S where they began to decline again. During the dry-season the highest SVPD values occured at around 14½°S, and the southern end of the transect had lower values than the northern end. Although the geographic location of the highest SVPD values varied throughout the year, the fact that the highest SVPD values occured in the middle of the transect results in a pattern of annual potential evaporation with a peak at 19½°S (Figure 6.1i).

The values of ω (Comstock & Ehleringer 1992), an index of evaporative demand weighted by moisture availability, were highest in the middle of the transect reflecting the patterns of SVPD (Figure 6.1j). The values started at around 45 Pa kPa^{-1} in the north, and then sharply increased between 14 and 15°S to over 50 Pa kPa^{-1}. From 15°S to 20°S the values continued to increase to near 55 Pa kPa^{-1}, and then declined to ~37.5 Pa kPa^{-1} from 23 to 25°S.

Transect zone means

As presented in other Chapters, the carbon isotope discrimination (Δ) recorded in both the leaf and wood tissues decreased linearly with latitude (Figure 6.2a). The Δ in wood tissues showed less variability within a zone, and was more closely correlated with latitude than was the leaf Δ, and both deviated most from the linear relationship at the drier end of the transect. Position along the transect accounted for 42% of the variability in the 645 samples of leaf Δ, and 60% of the variability in the equal number of wood samples. From the north to the south there was a decrease in mean Δ of 3.9‰ for both leaf and wood samples, and wood tissue was consistently 1.3‰ lower than leaf tissue (Figure 6.2b). The high variability in zone mean leaf and wood Δ south of 21.5°S was the result of only 1 or 2 species being present (Figure 6.2c); the tall tree *E. terminalis* and the mallee shrub *E. gamophylla*.

Mass-based leaf nitrogen concentrations were constant across the transect and averaged 8.4 mg g^{-1} (Figure 6.2d). Area-based nitrogen concentrations increased significantly ($P < 0.0001$) with latitude from around 1.15 to 3.06 gN m^{-2} (based on the end points of the linear regression) reflecting the changes in SLA (Figures 6.2e and 6.2f). Zone mean leaf carbon concentrations varied little across the transect, and averaged just over 500 mgC g^{-1} (Figure 6.2g).

The size of the sampled tree decreased with decreasing rainfall as measured by both the diameter of the trunk at breast height (approximately 1.5m) and the height of the canopy (Figures 6.2h and 6.2i). Neither measure showed great consistency, with DBH values being low at the northernmost zone which was recovering from cyclone damage, and in the south *E. terminalis* was a large tree.

From the specific leaf area and either the mass- or area-based leaf nitrogen concentrations, the calculated net photosynthetic capacities (on both mass- and area-bases; Reich et al. 1998) showed significant ($P<0.0001$) trends with latitude (Figures 6.3a and 6.3b). Zone mean calculated A_{mass} decreased from between 30 and 40 nmol g^{-1} s^{-1} to around 20 nmol g^{-1} s^{-1} from north to south, while the decrease in SLA reversed the trend for calculated A_{area} which increased from around 5 to around 6.5 μmol m^{-2} s^{-1}. Photosynthetic nitrogen-use efficiency (A_N) values reflect the SLA values as A_{mass} was calculated from SLA and N_{mass}, and A_N was calculated from A_{mass} and N_{mass}. Zone average A_N values were around 4 μmol gN^{-1} s^{-1} in the north and decreased to around 2.5 μmol gN^{-1} s^{-1} in the south. Leaf conductances, based on the calculated A_{area} and the leaf Δ values decreased significantly ($P < 0.0001$) from around 90 to around 70 mmol m^{-2} s^{-1} (Figure 6.3c). The patterns in the SVPD dominated the conductance values when calculating the transpiration rates (Figure 6.3d). The zone mean calculated E values increased from about 2 mmol m^{-2} s^{-1} in the north to around 3 mmol m^{-2} s^{-1} at the midpoint of the transect and then dropped to slightly below 2 mmol m^{-2} s^{-1} in the south. The ratio of calculated A_{area} to calculated E (a calculated instantaneous water-use efficiency value that is similar to the ratio of Δ to SVPD due to the methods used to calculate g as a function of A_{area} and Δ) mirrored the patterns of calculated E (Figure 6.3e). Overall, there was an increase in calculated water-use efficiency with increasing latitude. The overall response of A_{area}/E with latitude was stronger than the response of E, but the highest values were at both ends of the transect. Converting the instantaneous E values to an annual total (with the assumption of 8 hour days) predicts that around 480 mm of water will be transpired per unit leaf area across the transect. The ratio of annual total rainfall to annual total transpiration gives a crude estimate of an upper bound on the leaf area index along the transect, which varied from about 4 in the north to around 0.6 for all areas south of 17°S (Figure 6. 3f). The response of this upper bound on LAI was not linear, as it was determined by rainfall which distinctly decreased exponentially with latitude.

The ratio of the leaf carbon content to the assimilation rate (both mass-based), gives an estimate of the time required to recover the construction costs of the leaves. Assuming 8 hour days, it would require 40 to 50 days for the species at the northern end of the transect to accumulate the carbon that was in the leaves (Figure 6.3g). The leaf payback period increased to between 70 and 100 days in the species sampled at about 21 °S, and then slightly decreased again further south.

Correlates of leaf and wood Δ

The monthly values of most of the climate data show patterns where the trend with latitude reverses within the year over at least part of the transect (Figure 6.4). Whereas rainfall decreases from north to south in January, in July rainfall increases from north to south (Figure 6.4a). As a result, the leaf and wood Δ values, which decrease from north to south overall, tend to be positively correlated with monthly climate parameters during part of the year, and negatively correlated at other times within the year. For some parameters, such as rainfall where the amounts during the dry season are negligible, the biological significance of these reversing patterns may be limited while they do exhibit high correlation coefficients.

The leaf Δ of all of the *Eucalyptus* species sampled showed the highest positive correlations with: the natural log transformed mean annual rainfall (r = 0.65), the number of raindays in the wet season (r = 0.64), the maximum temperatures during the dry season (r = 0.62), rainfall during the wet season (r = 0.62), mean annual rainfall (r = 0.60), the number of raindays in the year (r = 0.59), incoming solar radiation during the dry season (r = 0.59), minimum temperatures during the dry season (r = 0.58), minimum temperatures during the transition seasons (r = 0.55), minimum temperatures during the whole year (r = 0.54), and the height of the canopy (r = 0.51) (Figure 6.5a). Leaf Δ values were correlated with wood Δ values (r = 0.71), the difference between the leaf and wood Δ values (r = 0.57), the calculated *g* values (r = 0.63), and the calculated transpiration rates during the dry season (r = 0.72).

The leaf Δ values showed the largest negative correlations with: the inverse of the mean annual rainfall (r = -0.66), potential evaporation during the wet season (r = -0.65), the annual average drought length (r = -0.64), the average drought length during the wet season (r = -0.63), the incoming solar radiation during the wet season (r = -0.61), the afternoon saturation vapor pressure deficit (r = -0.60), the potential evaporation for the whole year (r = -0.56), area-based leaf nitrogen contents (r = -0.56), area-based leaf carbon contents (r = -0.52), leaf mass per unit area (r = -0.51), and the potential evaporation during the transition seasons (r = -0.50). Leaf Δ values were also negatively correlated with latitude (r = -0.65) and site elevation (r = -0.62).

Wood Δ values showed stronger correlations than leaf Δ values in some cases, and were generally in the same rank sequence (Figure 6.5b). The strongest positive correlates with wood Δ were: natural log transformed mean annual rainfall (r = 0.75), the maximum temperatures during the dry season (r = 0.75), the number of raindays during the wet season (r = 0.74), the incoming solar radiation during the dry season (r = 0.73), the minimum temperatures during the dry season (r = 0.73), the rainfall during the wet season (r = 0.71), the minimum temperatures during the transition seasons (r = 0.71), the average minimum temperatures for the entire year (r = 0.70), the mean annual rainfall (r = 0.69), the number of raindays in the entire year (r = 0.67), the calculated transpiration rates during the dry season (r = 0.63), the maximum temperatures during the transition seasons (r = 0.62) and for the entire year (r = 0.59), the mid-afternoon saturation vapor pressure deficits during the dry season (r = 0.59), the rainfall during the transition seasons (r = 0.56), the drought lengths during the dry season (r = 0.55), and the specific leaf area (r = 0.50).

Wood Δ was most strongly negatively correlated with: the inverse of the mean annual rainfall (r = -0.77), the drought lengths during the wet season (r = -0.76), the potential evaporation during the wet season (r = -0.73), the annual average drought lengths (r = -0.71), the incoming solar radiation during the wet season (r = -0.71), the mid-afternoon saturation vapor pressure deficit during the wet season (r = -0.67), the number of raindays during the dry season (r = -0.61), the potential evaporation for the entire year (r = -0.60), the area-based leaf carbon content (r = -0.59), the leaf mass per unit area (r = -0.58), the number of raindays during the dry season (r = -0.55), the area-based leaf nitrogen contents (r = -0.54), and the potential evaporation during the transition seasons ($r = -0.51$). Wood Δ was also negatively correlated with the latitude of the sampling location ($r = -0.77$) and the elevation ($r = -0.74$).

The correlations between the leaf and wood Δ values of the individual species and the same suite of environmental, morphological, and calculated characteristics as were used for the complete data set show different patterns in both the strength and rank order of the correlations (Figures 6.6 and 6.7). The patterns of the correlations do not follow that of the complete overstory, nor do they resemble co-occurring species. Species that did not have significant changes in either leaf or wood Δ values across their distributions (i.e. were not correlated with latitude) were generally not correlated with many other characters. The leaf Δ values of *E. tetrodonta*, *E. tectifica*, *E. confertiflora*, and *E. coolabah* and the wood Δ values of *E. tectifica*, *E. confertiflora*, *E. chlorophylla*, *E. pachyphylla*, and *E. gamophylla* were not significantly correlated with latitude.

Regressions of leaf and wood Δ

As Δ theoretically reflects the balance between supply and demand for CO_2 during photosynthesis, regressions of Δ on calculated g and calculated A_{area} can determine the extent to which either parameter was limiting. It should be remembered that the calculated g was found from the calculated A_{area} and Δ in this data set. Without accounting for species differences (i.e. for the complete data set), the leaf Δ values were significantly ($P < 0.0001$) correlated with the calculated A_{area} values, although the r^2 was low (0.13). The correlation between leaf Δ and the calculated g values had a higher r^2 of 0.39. The mass-based calculated photosynthetic capacity was less related to leaf Δ than A_{area} ($r^2 = 0.02$), but was more related to wood Δ than A_{area} was (r^2 of 0.11 versus 0.05). The correlation between wood Δ and g was lower than between leaf Δ and g ($r^2 = 0.21$). Unfortunately, without an independant estimate of g it is not possible to contrast the importance of g versus A_{area} in determining patterns of leaf and wood Δ.

Of the many environmental factors that could limit the calculated g, a stepwise regression was used to isolate the significant parameters. The possible parameters for inclusion in the regression were the morphological measurements of the height of the top of the canopy and DBH, water availability (the monthly rainfall values, and sums for the wet season, the dry season, the transitional seasons, and the annual total), water demand (the monthly saturated vapor pressure deficits and potential evaporations, the averages of each for the three parts of the year, and the annual averages), the water availability weighted demand (ω), energy input for photosynthesis (the monthly average solar radiation, averages for the three parts of the year, and annual average), the monthly mean maximum and minimum temperatures, and the average drought length (monthly values and for the parts of the year) which could be a selection pressure for conservative water-use patterns. Without separating the values by species (*i.e.* for the full data set), the calculated g values were correlated with (having $P < 0.05$ to enter or exit the model); the height of the top of the canopy (partial correlation coefficient $r = -0.13$), the annual average drought length ($r = -0.08$), and average solar radiation in January and in November ($r = -0.13$, $r = 0.12$). The model had an r^2 of 0.14.

A stepwise regression was also used to determine the influences on the leaf and wood Δ values independently of the calculated g and A_{area} values. The same 107 parameters as in the earlier model were tested, as were the parameters related to calculating A_{area} (SLA, LMA, N_{mass}, N_{area}, C_{mass}, and C_{area}). Without separating the data by species, the leaf Δ values were correlated with; the number of raindays in February ($r = 0.30$), the annual average solar radiation ($r = 0.20$), rainfall in August ($r = 0.12$), LMA ($r = 0.10$), C_{mass} ($r = 0.06$), N_{mass} ($r = -0.09$), C_{area} ($r = -0.11$), the average drought length in May ($r = -0.11$), the number of raindays during the dry season ($r = -0.12$), SLA ($r = -0.13$) and the solar radiation in April ($r = -0.16$). The model had an r^2 of 0.53. Wood Δ values were correlated with; solar radiation in November ($r = 0.15$), the drought length in November ($r = 0.13$), the drought length in June ($r = 0.07$), solar radiation during the transition months ($r = -0.10$), the drought length in July ($r = -0.12$), DBH ($r = -0.145$), C_{mass} ($r = -0.22$), and latitude ($r = -0.24$). The model had an r^2 of 0.64.

Intra-specific trends

E. miniata and *E. tetrodonta*

Regressions of leaf Δ on calculated g or calculated A_{area} found the variability in leaf Δ in *E. miniata* was related to g ($r^2 = 0.50$; $P < 0.01$) and not related to A_{area}. Patterns of leaf Δ in *E. tetrodonta* were also not related to calculated A_{area}, but were correlated with calculated g ($r^2 = 0.52$; $P < 0.01$). Stepwise regressions of calculated g

on the same list of 107 parameters as in the zone means section found g correlated with the average drought length in February (partial $r^2 = 0.24$) and the evaporation in October (partial $r^2 = 0.06$) in the case of *E. miniata*, and to the average rainfall in August ($r^2 = 0.47$) in the case of *E. tetrodonta*. The calculated g of *E. miniata* was negatively correlated with the February drought length and the October evaporation, and the calculated g of *E. tetrodonta* was positively correlated with the August rainfall. The stepwise regression of leaf and wood Δ with the list of 113 parameters specified in the zone means section found the average drought length in the transitional months (partial $r^2 = 0.19$) and solar radiation in May (partial $r^2 = 0.15$) correlated to *E. miniata* leaf Δ, and mid-afternoon SVPD in May (partial $r^2 = 0.44$), DBH (partial $r^2 = 0.06$), and May rainfall (partial $r^2 = 0.05$) were correlated to wood Δ. Leaf Δ was negatively correlated with the transitional season drought length, and positively correlated with the May solar radiation. Wood Δ was negatively correlated with both May SVPD and DBH, and positively correlated with May rainfall. *E. tetrodonta* leaf Δ correlated with the minimum temperatures in January (partial $r^2 = 0.41$), and C_{mass} (partial $r^2 = 0.09$). *E. tetrodonta* wood Δ correlated with mean maximum temperatures in August (partial $r^2 = 0.34$), height of the top of the canopy (partial $r^2 = 0.06$), N_{mass} (partial $r^2 = 0.04$), solar radiation in the transitional months (partial $r^2 = 0.34$), and solar radiation in June (partial $r^2 = 0.05$). Leaf Δ was positively correlated to January minimum temperatures, and negatively correlated to C_{mass}. Wood Δ was negatively correlated to August maximum temperatures, the canopy height, and solar radiation in the transitional months, and positively correlated with N_{mass} and solar radiation in June.

E. tectifica and *E. chlorophylla*

Leaf Δ values of *E. tectifica* and *E. chlorophylla* were unrelated to calculated A_{area}, but were significantly correlated to calculated g (r^2 values of 0.38 and 0.30; $P = 0.015$ and $P < 0.01$ respectively). In *E. tectifica* the calculated g values were correlated with the potential evaporation in May (partial $r^2 = 0.67$), the rainfall in December (partial $r^2 = 0.12$), and the solar radiation in the transitional months (partial $r^2 = 0.04$), while none of the environmental parameters correlated with the patterns of calculated g in *E. chlorophylla*. The calculated g of *E. tectifica* was negatively correlated with the evaporation in May and the solar radiation in the transitional months, and positively correlated with December rainfall. The leaf Δ values of *E. tectifica* were negatively correlated with the minimum temperatures in the transitional months (partial $r^2 = 0.44$) and negatively correlated with the minimum temperatures in the wet season (partial $r^2 = 0.20$). The wood Δ values of *E. tectifica* were positively correlated with the evaporation in September (partial $r^2 = 0.28$). In *E. chlorophylla* the leaf Δ values were negatively correlated with the leaf carbon content ($r^2 = 0.33$) and the wood Δ values were not correlated with any of the possible parameters.

E. confertiflora

Leaf Δ values of *E. confertiflora* were not correlated to the calculated A_{area} values, but were correlated with the calculated g values ($r^2 = 0.30$, $P < 0.01$). Calculated g values were negatively correlated with rainfall in June (partial $r^2 = 0.12$), positively correlated with solar radiation on July (partial $r^2 = 0.07$), and negatively correlated with the SVPD during the transitional months (partial $r^2 = 0.10$). Leaf Δ was not correlated with any of the possible parameters, and wood Δ was negatively correlated with the inverse of SLA (g{leaf} m^{-2})(partial $r^2 = 0.12$).

E. pruinosa, *E. coolabah*, and *E. leucophloia*

Leaf Δ values of *E. pruinosa* were correlated ($P < 0.01$) with both the calculated A_{area} ($r^2 = 0.18$) and calculated g ($r^2 = 0.62$), while in *E. coolabah* and *E. leucophloia* they were only correlated with g ($r^2 = 0.60$ and $r^2 = 0.61$). The variability in calculated g of *E. pruinosa* was negatively correlated with the drought length in April ($r^2 = 0.28$). The variability in calculated g of *E. coolabah* was correlated with the mean minimum temperatures in December (partial $r^2 = 0.36$), and the rainfall in May (partial $r^2 = 0.08$). The calculated g was negatively correlated with December minimum temperatures, and positively correlated with May rainfall. The variability in calculated g of *E. leucophloia* was correlated with the drought length in April ($r^2 = 0.33$). The leaf Δ values of *E. pruinosa* were correlated with the rainfall in June (partial $r^2 = 0.45$), the mean maximum temperatures in November (partial $r^2 = 0.08$), and N_{area} (partial $r^2 = 0.04$). Leaf Δ values were negatively correlated with June rainfall and N_{area}, and positively correlated with November maximum temperatures. The wood Δ values of *E. pruinosa* were negatively correlated with the mean maximum temperatures in the wet season ($r^2 = 0.25$). In *E.*

coolabah the leaf Δ values were correlated with the mean minimum temperatures in December (partial $r^2 = 0.40$), the rainfall in July (partial $r^2 = 0.08$), DBH (partial $r^2 = 0.10$), SLA (partial $r^2 = 0.06$), and the rainfall in June (partial $r^2 = 0.05$). Leaf Δ was negatively correlated with the minimum temperatures in December, SLA, and June rainfall, and positively correlated with the July rainfall and DBH. Wood Δ values of *E. coolabah* were negatively correlated with the rainfall in July (partial $r^2 = 0.22$). In *E. leucophloia* leaf Δ values were positively correlated with rainfall in February (partial $r^2 = 0.50$) and DBH (partial $r^2 = 0.05$), and wood Δ was positively correlated with the rainfall in December (partial $r^2 = 0.44$) and DBH (partial $r^2 = 0.05$).

E. dichromophloia and *E. terminalis*

Leaf Δ of both *E. dichromophloia* and *E. terminalis* correlated with both the calculated A_{area} and the calculated g ($P < 0.01$). In both species the correlations with calculated A_{area} (*E. dichromophloia* $r^2 = 0.08$, *E. terminalis* $r^2 = 0.13$) were not as strong as with calculated g (*E. dichromophloia* $r^2 = 0.29$, *E. terminalis* $r^2 = 0.32$). In *E. dichromophloia* the calculated g correlated with the rainfall in August (partial $r^2 = 0.05$), the mean maximum temperatures in October (partial $r^2 = 0.07$), the SVPD in September (partial $r^2 = 0.07$), and the rainfall in September (partial $r^2 = 0.05$). The correlations with August rainfall and October maximum temperatures were positive, and the correlations with September SVPD and September rainfall were negative. In *E. terminalis* the calculated g was positively correlated with both the drought length in August ($r^2 = 0.06$), and the mean minimum temperatures in September. *E. dichromophloia* leaf Δ values were correlated with the mean minimum temperatures in May (partial $r^2 = 0.20$), the height of the trees (partial $r^2 = 0.04$), and rainfall in September (partial $r^2 = 0.05$). The correlations with May minimum temperatures and tree height were positive, while the correlations with September rainfall was negative. *E. dichromophloia* wood Δ values were correlated with the mean minimum temperatures in July (partial $r^2 = 0.44$), the rainfall in July (partial $r^2 = 0.07$), DBH (partial $r^2 = 0.04$), and the rainfall in October (partial $r^2 = 0.06$). The correlations with July minimum temperatures, DBH, and October rainfall were positive, while the correlation with July rainfall were negative. Leaf Δ values of *E. terminalis* were correlated with the drought length in August (partial $r^2 = 0.23$), the rainfall in August (partial $r^2 = 0.11$), N_{mass} (partial $r^2 = 0.09$), the rainfall in

September (partial $r^2 = 0.07$), and ω (partial $r^2 = 0.04$). The correlations with the drought length in August and ω were positive, and the correlations with August rainfall, N_{mass}, and September rainfall were negative. Wood Δ values of *E. terminalis* were correlated with the SVPD in August (partial $r^2 = 0.49$), the rainfall in during the dry season (partial $r^2 = 0.05$), the average solar radiation in November (partial $r^2 = 0.04$), and N_{mass} (partial $r^2 = 0.02$). The correlations with August SVPD was positive, and the other correlations were negative.

E. odontocarpa, *E. pachyphylla*, and *E. gamophylla*

Leaf Δ values of *E. odontocarpa* and *E. pachyphylla* were correlated with calculated *g* ($r^2 = 0.39$ and 0.40, $P < 0.01$ in both cases) , but not with calculated A_{area}, while in *E. gamophylla* leaf Δ values were correlated with calculated A_{area} ($r^2 = 0.32$, $P < 0.01$) and not with calculated *g*. The calculated *g* values of *E. odontocarpa* and *E. pachyphylla* were not correlated with any of the possible driving variables at the threshold sensitivity of the stepwise regression ($P < 0.05$). The calculated *g* values of *E. odontocarpa* were positively correlated with the rainfall in September (partial $r^2 = 0.13$), and the rainfall in the wet season (partial $r^2 = 0.13$). Leaf Δ values of *E. odontocarpa* were positively correlated with the average drought length in September ($r^2 = 0.22$), and wood Δ values were positively correlated with ω (partial $r^2 = 0.48$), and the annual average SVPD (partial $r^2 = 0.10$). The leaf Δ values of *E. pachyphylla* were positively correlated with both the annual average solar radiation (partial $r^2 = 0.22$), and evaporation in December (partial $r^2 = 0.11$). The wood Δ values of *E. pachyphylla* were negatively correlated with C_{mass} ($r^2 = 0.33$). Leaf Δ of *E. gamophylla* was correlated with the average solar radiation in the wet season (partial $r^2 = 0.36$), N_{area} (partial $r^2 = 0.21$), and rainfall in February (partial $r^2 = 0.09$). The correlation with wet season rainfall was positive, and the correlations with N_{area} and February rainfall were negative. Wood Δ of *E. gamophylla* was correlated with the solar radiation in February (partial $r^2 = 0.18$), the rainfall in April (partial $r^2 = 0.19$), and DBH (partial $r^2 = 0.11$). The correlations with February solar radiation and April rainfall were positive, and the correlation with DBH was negative.

6.4 Discussion

The transect through the bio-climatic gradient from Darwin to the southern border of the Northern Territory is marked by a strong gradient in the total annual rainfall and in the seasonality of the rainfall. The monthly mean statistics can differentiate the wettest four months and the driest four months leaving two 2 month transitional periods which where combined. This is a simplistic analysis of the dynamics of the Australian wet-dry tropics where six seasons can be identified (Braithwaite & Estbergs 1988), and where extreme events are probably as important as long-term means (Taylor & Tulloch 1985). Intra-annual subtleties, such as the decreases in VPD which precede the breaking of the drought and may be important phenological cues (Duff et al. 1997), are also missing. The gradient in mean SVPD changes from increasing from north to south during the wet season, to decreasing from north to south in the dry season, and ω (Comstock & Ehleringer 1992),which weights VPD by moisture availability, was highest in the middle of the transect. The result is a complex environmental gradient between the north coast and the center of Australia involving most of the climatic variables which could influence plant survival and growth in non-linear and changing combinations.

There was a tight, linear decrease of both leaf and wood Δ and increasing latitude (from north to south) in the sampled overstory *Eucalyptus* species. Area-based leaf nitrogen contents increased, which were matched by the increase in leaf-mass per unit area such that the mass-based leaf nitrogen contents did not show a trend across the transect. Overall, the area-based calculated assimilation capacities (Reich et al. 1998) were correlated with the leaf Δ values, but this was only found in 4 of the 13 individual species. Leaf Δ values correlated with the calculated leaf conductances in 8 of the 13 species, but g was calculated from the ratio of A to Δ. Carbon isotope discrimination was found to reflect leaf nitrogen contents in riparian vegetation along an elevation gradient (Sparks & Ehleringer 1997). In these stream-side trees the increase in LMA and area-based leaf nitrogen contents correlated with decreasing Δ values reflecting proposed increasing assimilation capacities with an assumed minimal decrease in leaf conductances.

Not having a method to independently measure or estimate *g* meant it was not possible to either translate photosynthetic capacity into a measure of long term average photosynthetic performance, which might show a stronger correlation with Δ, or establish the relative importance of *g* versus *A* in determining Δ values. However, factors that relate to the water economies of the trees consistently showed higher correlations with Δ values than did leaf nitrogen contents, which would indicate *g* could be more important than *A* in determining Δ values.

The tight, linear relationship between both zone mean leaf Δ and zone mean wood Δ values and latitude, and the non-linear pattern of mean annual rainfall with latitude, resulted in a non-linear response of Δ to rainfall similar to that found in the same area of the Northern Territory by Schulze *et al.* (1998). This non-linear response of Δ to water availability differs from the linear relationship between mean annual rainfall and community average Δ found in Queensland by Stewart *et al.* (1995), but does follow other reported non-linear responses (Lajtha & Getz 1993; Korol et al. 1999).

Although there is an 8-fold gradient in mean annual rainfall across this transect, along the full length of the transect there is at least a 3 month dry season with essentially no rainfall. Overstory trees therefore either have roots at depths to reach a permanent water table, or will experience a period of limited water supply every year, regardless of their position along the transect. The inter-annual variation in the depth of the water table, and a series of low rainfall years, may limit the distributions of species by direct mortality, while not generating a consistent annual decrease in *g* and therefore Δ. Species distributions are also probably strongly determined during the establishment phase, and young trees may require a series of exceptionally wet years in order to grow roots deep enough to reach the dry season water table, as well as to avoid the annual fire cycle.

In order to maximize their carbon-gain, plants should regulate their water-use so that they just exhaust their supply at end of the average interval between rain events (i.e. over the average drought length) (Berninger, Makela & Hari 1996; Makela, Berninger & Hari 1996). This "forward-planning" could be expected to arise in populations which have experienced multiple generations under a similar climatic regime, as in the

Northern Territory (Pole & Bowman 1996). Leaf conductances, and therefore Δ values, should decrease as the drought interval increases in length. Overall, both the leaf and wood Δ values showed strong negative correlations with the annual average drought lengths, as well as the drought lengths during the wet season in isolation (Figure 6.5). There were significant correlations between the two drought lengths and leaf Δ for 6 species, and with wood Δ for 9 species.

Stewart *et al.* (1995) also found that the number of rain days per year was linearly related to Δ, with correlation coefficients as high as found with mean annual rainfall. Although they analyzed their community average Δ values in terms of the mean annual rainfall during the 5 years before sample collection, and the long-term averages (with r^2 values of 0.70 and 0.78 respectively), they also found there was a correlation with the number of raindays per annum ($r^2 = 0.70$). Along their transect and along this transect the annual average drought lengths varied between around 2.5 and 8 days. At sites with the longer drought lengths, both transects found similar leaf Δ values (~18‰), but at sites with annual average drought lengths of 2.5 days the leaf Δ values in the Northern Territory were around 21‰, while in Queensland they reached 24‰. The differences are could be due to the fact that Stewart *et al.* (1995) sampled a wider range of growth-forms, including co-occurring understory species which may have higher Δ values (Brooks et al. 1997; Pate et al. 1998).

Although the annual average SVPD or the SVPD during at least one season, which should influence *g* and therefore Δ (Lloyd & Farquhar 1994), was significantly correlated with both leaf and wood Δ values overall, and in the cases of the leaf Δ of 9 species and the wood Δ of 8 species, other parameters had higher correlations. Along a rainfall gradient in Oregon, USA, VPD and soil drought explained 69% of the between site variability in whole tissue $\delta^{13}C$ after being corrected for branch length based on the analysis of the parameters in the FOREST-BGC model that constrain transpiration (Panek & Waring 1995). VPD and the modeled ratio of actual transpiration to potential transpiration were significantly correlated ($P<0.0001$) with differences in foliar $\delta^{13}C$ cellulose between years within a site, but none of the climatic constrains on conductance were significantly correlated with annual ring wood cellulose $\delta^{13}C$ (Panek & Waring 1997).

Williams and Ehleringer (1996) found interspecific differences in the patterns of Δ values across an environmental gradient where growing season rainfall and vapor pressure deficits increased together. They sampled whole leaf Δ of *Quercus gambelii*, *Pinus edulis*, and *Juniperus osteosperma* at 6 sites in Utah and Arizona with annual rainfalls between 350 and 500 mm yr^{-1}, and where summer rainfall increased from 18 to 58%. Growing season evaporative demand tracked summer rainfall, so that there was a strong gradient in ω, an index of evaporative demand weighted by moisture availability (Comstock & Ehleringer 1992). It was hypothesized that the gradient in evaporative demand would be stronger than the gradient in summer moisture supply, and that stomatal closure (as a result of VPD) would lead to a negative relationship between Δ and summer rainfall amounts (i.e. that plants would exhibit greater water stress and stomatal limitation with higher rainfall). Of the three species, the leaf Δ of *Quercus* correlated with ω, while the leaf Δ of *Juniperus* correlated with summer rainfall, and *Pinus* exhibited no correlations. Both of the conifers add late season wood with summer rainfall events, which would increase the hydraulic conductivity and maintain leaf conductances under increased VPD, while *Quercus* was less morphologically plastic, and relied on stomatal control to mediate water loss under higher VPD.

Along the gradient in the Northern Territory ω did not respond linearly with latitude and therefore did not correlate well with Δ values. Along parts of the gradient where the trend in ω was linear with latitude, significant correlations existed with the leaf Δ of 7 species and the wood Δ of 6 species.

Because of the strong covariance in all of the climatic parameters the regression models found the strongest single correlate, but then could not fit many more parameters. The different species tended to have differing parameters with the strongest correlation, so the regression models do not show consistent patterns in their structure. Isolating, and then ranking the importance of the potential influences on the supply of, and demand for water, as well as the influences on photosynthetic rates was not particularly successful. The changes in the importance of the influences on Δ across the transect were also not clear. Monthly mean climatic data may not correlate well with plant performance in an environment where the diurnal variations in measures such as air temperatures are greater than the annual variation in daily maximum temperature.

6.5 Literature Cited

Berninger, F., Makela, A. & Hari, P. (1996) Optimal control of gas exchange during drought: Empirical evidence. Annals of Botany 77, 469-476.

Braithwaite, R. & Estbergs, J. (1988) Tuning in to the six seasons of the wet-dry tropics. Australian Natural History 22, 444-449.

Brooks, J.R., Flanagan, L.B., Buchmann, N. & Ehleringer, J.R. (1997) Carbon isotope composition of boreal plants: functional groupings of life forms. Oecologia 110, 301-311.

Comstock, J.P. & Ehleringer, J.R. (1992) Correlating genetic variation in carbon isotopic composition and complex climatic gradients. Proceedings of the National Academy of Science 89, 7747-7751.

Duff, G.A., Myers, B.A., Williams, R.J., Eamus, D., O'Grady, A. & Fordyce, I.R. (1997) Seasonal patterns in soil moisture, vapour pressure deficit, tree canopy cover and pre-dawn water potential in a northern Australian savanna. Australian Journal of Botany 45, 211-224.

Ehleringer, J.R. & Cook, C.S. (1990) Characteristics of *Encelia* species differing in leaf reflectance and transpiration rate under common garden conditions. Oecologia 82, 484-489.

Farquhar, G.D., O'Leary, M.H. & Berry, J.A. (1982) On the relationship between carbon isotope discrimination and the intercellular carbon dioxide concentration in leaves. Australian Journal of Plant Physiology 9, 121-137.

Korol, R.L., Kirschbaum, M.U.F., Farquhar, G.D. & Jeffreys, M. (1999) Effects of water status and soil fertility on the C-isotope signature in *Pinus radiata*. Tree Physiology 19, 551-562.

Lajtha, K. & Getz, J. (1993) Photosynthesis and water-use efficiency in pinyon-juniper communities along an elevation gradient in northern New Mexico. Oecologia 94, 95-101.

Lloyd, J. & Farquhar, G.D. (1994) ^{13}C discrimination during CO_2 assimilation by the terrestrial biosphere. Oecologia 99, 201-205.

Makela, A., Berninger, F. & Hari, P. (1996) Optimal control of gas exchange during drought: Theoretical analysis. Annals of Botany 77, 461-467.

Miller, J.M., Williams, R.J. & Farquhar, G.D. (2001) Carbon isotope discrimination by a sequence of *Eucalyptus* species along a subcontinental rainfall gradient in Australia. Functional Ecology 15, 222-232.

Panek, J. & Waring, R.H. (1997) Stable carbon isotopes as indicators of limitations to forest growth imposed by climate stress. Ecological Applications 7, 854-863.

Panek, J.A. & Waring, R.H. (1995) Carbon isotope variation in Douglas-fir foliage: improving the ^{13}C-climate relationship. Tree Physiology 15, 657-663.

Pate, J.S., Unkovich, M.J., Erskine, P.D. & Steward, G.R. (1998) Australian mulga ecosystems - ^{13}C and ^{15}N natural abundances of biota components and their ecophysiological significance. Plant, Cell and Environment 21, in press.

Pole, M.S. & Bowman, D.M.J.S. (1996) Tertiary plant fossils from Australia's 'Top End'. Australian Systematic Botany 9, 113-126.

Reich, P.B., Ellsworth, D.S. & Walters, M.B. (1998) Leaf structure (specific leaf area) modulates photosynthesis-nitrogen relations: evidence from within and across species and functional groups. Functional Ecology 12, 948-958.

Ryan, M.G. & Yoder, B.J. (1997) Hydraulic limits to tree height and tree growth. BioScience 47, 235-242.

Schmidt, H.-L. & Gleixner, G. (1998) Carbon isotope effects on key reactions in plant metabolism and ^{13}C-patterns in natural compounds. In: Stable Isotopes: integration of biological, ecological and geochemical processes (H. Griffiths), 13-25. BIOS Scientific Publishers Ltd., Oxford.

Schulze, E.-D., Williams, R.J., Farquhar, G.D., Schulze, W., Langridge, J., Miller, J.M. & Walker, B.H. (1998) Carbon and nitrogen isotope discrimination and nitrogen nutrition of trees along a rainfall gradient in northern Australia. Australian Journal of Plant Physiology 25, 413-425.

Sparks, J.P. & Ehleringer, J.R. (1997) Leaf carbon isotpe discrimination and nitrogen content for riparian trees along elevational transects. Oecologia 109, 362-367.

Stewart, G.R., Turnbull, M.H., Schmidt, S. & Erskine, P.D. (1995) ^{13}C natural abundance in plant communities along a rainfall gradient: a biological integrator of water availability. Australian Journal of Plant Physiology 22, 51-55.

Taylor, J.A. & Tulloch, D. (1985) Rainfall in the wet-dry tropics: Extreme events at Darwin and similarities between years during the period 1870-1983 inclusive. Australian Journal of Ecology 10, 281-295.

Virgona, J.M. & Farquhar, G.D. (1996) Genotypic variation in relative growth rate and carbon isotope discrimination in sunflower is related to photosynthetic capacity. Australian Journal of Plant Physiology 23, 227-236.

Williams, D.G. & Ehleringer, J.R. (1996) Carbon isotope discrimination in three semi-arid woodland species along a monsoon gradient. Oecologia 106, 455-460.

6.6 Tables and Figures

Table 6.1a Sampling locations across the distributions of the species in the northern half of the transect.

Zone name	E. miniata	E. tetrodonta	E. tectifica	E. dichromophloia	E. confertiflora	E. chlorophylla	E. pruinosa	E. leucophloia QQ	E. terminalis	E. coolibah	E. odontocarpa	E. pachyphylla	E. gamophylla
Darwin Radio Beacon	S 12° 25.79' E 130° 57.46'	S 12° 25.53' E 130° 57.35'											
Acacia Shop	S 12° 49.62' E 131° 8.04'	S 12° 49.62' E 131° 8.04'											
Site 3	S 13° 4.28' E 131° 6.18'		S 13° 4.38' E 131° 6.13'										
Site 4	S 13° 25.66' E 131° 18.54'	S 13° 28.09' E 131° 19.71'	S 13° 28.09' E 131° 19.71'										
Hayes Creek	S 13° 41.70' E 131° 41.43'	S 13° 41.66' E 131° 41.48'		S 13° 37.51' E 131° 35.34'	S 13° 41.51' E 131° 41.35'								
Cullen Creek	S 13° 59.59' E 131° 55.56'		S 13° 57.85' E 131° 54.37'	S 14° 4.08' E 131° 58.47'	S 14° 2.04' E 131° 56.76'								
Edith Farms	S 14° 19.20' E 132° 6.54'	S 14° 17.90' E 132° 5.18'	S 14° 19.05' E 132° 6.41'	S 14° 14.62' E 132° 3.07'	S 14° 20.46' E 132° 7.71'								
Katherine	S 14° 34.96' E 132° 31.04'	S 14° 32.94' E 132° 26.97'	S 14° 29.10' E 132° 24.04'	S 14° 32.94' E 132° 26.97'	S 14° 32.94' E 132° 26.97'								
Central Arnhem Hwy	S 14° 45.55' E 132° 51.13'	S 14° 45.55' E 132° 51.13'	S 14° 43.19' E 132° 48.88'	S 14° 45.55' E 132° 51.13'	S 14° 45.55' E 132° 51.13'	S 14° 43.08' E 132° 48.67'							
Elsey RIver	S 15° 12.23' E 133° 6.16'	S 15° 11.03' E 133° 5.86'		S 15° 11.03' E 133° 5.86'	S 15° 11.03' E 133° 5.86'	S 15° 11.03' E 133° 5.86'	S 15° 4.35' E 133° 4.24'						
Larrimah	S 15° 30.04' E 133° 11.85'	S 15° 32.24' E 133° 12.32'		S 15° 33.49' E 133° 12.55'	S 15° 34.68' E 133° 13.06'	S 15° 35.47' E 133° 13.46'	S 15° 41.16' E 133° 18.32'	S 15° 38.81' E 133° 16.33'	S 15° 43.49' E 133° 21.13'	S 15° 46.54' E 133° 22.63'			
16°S				S 15° 54.89' E 133° 25.51'	S 16° 7.76' E 133° 25.68'	S 15° 53.26' E 133° 24.80'	S 16° 4.18' E 133° 25.97'	S 16° 6.72' E 133° 25.75'	S 16° 7.76' E 133° 25.68'	S 16° 7.76' E 133° 25.68'			
Buchanan Hwy				S 16° 36.31' E 133° 21.66'	S 16° 21.11' E 133° 22.83'		S 16° 24.28' E 133° 22.64'	S 16° 36.31' E 133° 21.66'	S 16° 39.07' E 133° 23.35'	S 16° 28.12' E 133° 23.33'			
Shenandoah				S 16° 54.70' E 133° 25.42'	S 16° 51.96' E 133° 25.51'					S 16° 51.25' E 133° 25.60'			
Newcastle Waters				S 17° 22.40' E 133° 26.30'			S 17° 13.32' E 133° 28.19'		S 17° 30.00' E 133° 30.53'	S 17° 22.10' E 133° 25.96'			
Barkley Stock Route				S 17° 44.89' E 133° 38.45'			S 17° 42.44' E 133° 37.78'	S 17° 56.65' E 133° 42.83'	S 17° 41.67' E 133° 37.61'				
Renner Springs				S 18° 17.91' E 133° 47.03'			S 18° 17.91' E 133° 47.03'	S 18° 17.91' E 133° 47.03'	S 18° 16.77' E 133° 46.49'	S 18° 8.40' E 133° 43.57'			

Table 6.1b Sampling locations across the distributions of the species in the southern half of the transect.

Zone name	E. miniata	E. tetrodonta	E. tectifica	E. dichromophloia	E. confertiflora	E. chlorophylla	E. pruinosa	E. leucophloia QQ	E. terminalis	E. coolibah	E. odontocarpa	E. pachyphylla	E. gamophylla
Muckaty Stn				S 18° 37.93' E 133° 56.83'			S 18° 37.93' E 133° 56.83'	S 18° 37.93' E 133° 56.83'	S 18° 37.93' E 133° 56.83'	S 18° 32.50' E 133° 53.98'	S 18° 37.93' E 133° 56.83'		
Attack Creek				S 18° 55.07' E 134° 6.97'			S 19° 0.93' E 134° 8.36'	S 19° 3.70' E 134° 9.60'	S 19° 3.70' E 134° 9.60'	S 19° 3.70' E 134° 9.60'	S 19° 3.70' E 134° 9.60'		
3 Ways							S 19° 31.32' E 134° 13.27'	S 19° 28.68' E 134° 12.88'	S 19° 31.32' E 134° 13.27'		S 19° 31.32' E 134° 13.27'	S 19° 21.93' E 134° 11.72'	
Tennant Creek							S 19° 41.79' E 134° 10.63'	S 19° 41.79' E 134° 10.63'	S 19° 51.59' E 134° 12.19'		S 19° 41.79' E 134° 10.63'		
Edinburgh Creek								S 20° 30.55' E 134° 15.68'	S 20° 2.33' E 134° 12.42'		S 20° 8.41' E 134° 13.30'	S 20° 17.41' E 134° 13.77'	
Devils Marbles									S 20° 36.11' E 134° 13.96'		S 20° 36.11' E 134° 13.96'	S 20° 37.07' E 134° 13.18'	
Warribri									S 20° 6.28' E 134° 10.05'			S 21° 6.24' E 134° 10.09'	S 21° 19.16' E 134° 2.07'
Barrow Ck									S 21° 35.87' E 133° 45.91'			S 21° 35.21' E 133° 46.63'	
Hansens Well									S 21° 56.29' E 133° 31.56'			S 21° 56.29' E 133° 31.56'	
Tea Tree									S 22° 18.30' E 133° 24.61'				
Native Gap									S 22° 48.40' E 133° 25.17'				S 22° 50.59' E 133° 27.06'
Plenty Hwy									S 23° 7.85' E 133° 41.84'				
Tanami Rd									S 23° 28.24' E 133° 50.57'				
Alice									S 24° 2.30' E 133° 38.15'				S 24° 2.71' E 133° 37.87'
Jims Place									S 24° 20.72' E 133° 26.86'				S 24° 20.72' E 133° 26.86'
Erldunda													S 24° 54.87' E 133° 11.86'

Table 6.2 Biotic parameters used in the correlation analyses.

Variable	Definition
LEAF_D	Leaf Δ (‰)
WOOD_D	Wood Δ (‰)
DIFF_D	The difference between leaf Δ and wood Δ (Leaf Δ - Wood Δ; ‰)
SLA	Specific leaf area (m^2 kg^{-1})
GLEAFM2	Leaf mass per unit area (g m^{-2})
N_MASS	Mass-based leaf nitrogen content (mg g^{-1})
GNM2	Area-based leaf nitrogen content (g m^{-2})
C_MASS	Mass-based leaf carbon content (mg g^{-1})
GCM2	Area-based leaf carbon content (g m^{-2})
A_AREA	Calculated area-based potential leaf photosynthetic capacity (μmol m^{-2} s^{-1})
A_MASS	Calculated mass-based potential leaf photosynthetic capacity (nmol g^{-1} s^{-1})
G	Calculated leaf conductance to water vapour (mmol m^{-2} s^{-1})
E_WET	Calculated transpiration rate during wet season (mmol m^{-2} s^{-1})
E_DRY	Calculated transpiration rate during dry season (mmol m^{-2} s^{-1})
E_TR	Calculated transpiration rate during transition seasons (mmol m^{-2} s^{-1})
E_YR	Calculated annual transpiration rate (mmol m^{-2} s^{-1})
E_MM_YR	Calculated annual total transpiration (mm yr^{-1})
DBH	Trunk diameter at breast height (mm)
CROWNTOP	Height of top of leaf canopy (m)
CROWNBAS	Height of bottom of leaf canopy (m)
LAI	Calculated potential maximum leaf area index (m m^{-1})
PAYBACK	Calculated time to recover carbon content in leaves (days)

Table 6.3 Environmental parameters used in the correlation analyses.

Variable	Definition
DEM	Sample location elevation from a digital elevation map of Australia (m)
LAT2	Latitude of sample location (°S)
RAIN_WET	Mean rainfall during the wet season (December to March) (mm)
RAIN_DRY	Mean rainfall during the dry season (June to September) (mm)
RAIN_TR	Mean rainfall during the two transition seasons (October, November, and April, May; mm)
RAIN_YR	Mean annual rainfall (mm)
RAINYRM	Mean annual rainfall in meters (m)
L_RAIN_Y	Log_e mean annual rainfall
INV_R_M	Inverse of mean annual rainfall
RDAY_WET	Number of days with rainfall during the wet season (days)
RDAY_DRY	Number of days with rainfall during the dry season (days)
RDAY_TR	Number of days with rainfall during the transition seasons (days)
RDAY_YR	Number of days with rainfall during the year (days)
DRLN_WET	Mean drought length (number of days between rainfalls) during wet season (days)
DRLN_DRY	Mean drought length during dry season (days)
DRLN_TR	Mean drought length during transition seasons (days)
DRLN_YR	Mean drought length for entire year (days)
RAD_WET	Mean daily solar radiation during wet season (MJ m^{-2} d^{-1})
RAD_DRY	Mean daily solar radiation during dry season (MJ m^{-2} d^{-1})
RAD_TR	Mean daily solar radiation during transition seasons (MJ m^{-2} d^{-1})
RAD_YR	Mean annual daily solar radiation (MJ m^{-2} d^{-1})
EVAP_WET	Mean potential evaporation during wet season (mm)
EVAP_DRY	Mean potential evaporation during dry season (mm)
EVAP_TR	Mean potential evaporation during transition seasons (mm)
EVAP_YR	Mean annual potential evaporation (mm)

Table 6.3 continued.

Variable	Definition
TMAX_WET	Mean maximum air temperature during wet season (°C)
TMAX_DRY	Mean maximum air temperature during dry season (°C)
TMAX_TR	Mean maximum air temperature during transition seasons (°C)
TMAX_YR	Mean maximum annual air temperature (°C)
TMIN_WET	Mean minimum air temperature during wet season (°C)
TMIN_DRY	Mean minimum air temperature during dry season (°C)
TMIN_TR	Mean minimum air temperature during transition seasons (°C)
TMIN_YR	Mean minimum annual air temperature (°C)
VPD15WET	Calculated mean afternoon saturated vapor pressure deficit during wet season (kPa)
VPD15DRY	Calculated mean afternoon saturated vapor pressure deficit during dry season (kPa)
VPD15TR	Calculated mean afternoon saturated vapor pressure deficit during transition seasons (kPa)
VPD15YR	Calculated mean annual afternoon saturated vapor pressure (kPa)
OMEG_YR	Calculated annual index weighting demand for water with its availability (Comstock & Ehleringer 1992)

Figure Legends

Figure 6.1

The predicted physical and climatic parameters at the 97 sites of collection (ANUCLIM 1.8, Centre for Resource and Environmental Studies, ANU)). In all panels the wet-season values (December to March) are given by the open circle (○), the dry-season (June - September) values by the cross (X), the combined two transition seasons (April - May, October - November) by the open triangle (Δ), and the annual values by the closed circle (●). There is an exponential relationship ($W = 226.33784 + 1399.95313\ e^{-((L-12.4255)/2.98815)}$; $r^2 = 0.996$) between latitude (L) and mean annual rainfall (W) (not shown). The average drought length during a month was calculated as (days in month/raindays) -1. Saturation vapor pressure deficits and ω were calculated from ANUCLIM parameters as described in the methods.

Figure 6.2

The mean (± SE) measured values of all of the species occurring within each of the 50 km zones along the transect. The lines denote significant linear relationships ($\alpha = 0.05$).

Figure 6.3

The mean (± SE) calculated values of all of the species occurring within each of the 50 km zones along the transect.

Figure 6.4

The predicted monthly climatic parameters for January and July.

Figure 6.5

The correlation coefficients between leaf and wood Δ of all of the species combined and the available climatic and morphological parameters. The sequence of the parameters in this and subsequent figures is based on the values of the correlations with the full leaf Δ data set. In this and subsequent figures the correlations greater or equal to the vertical lines are significant at $\alpha = 0.05$.

Figure 6.6

The correlation coefficients between leaf Δ and the available climatic and morphological parameters for the individual species. The sequence of parameters is the same as in Figure 6.5.

Figure 6.7

The correlation coefficients between wood Δ and the available climatic and morphological parameters for the individual species. The sequence of parameters is the same as in Figure 6.5.

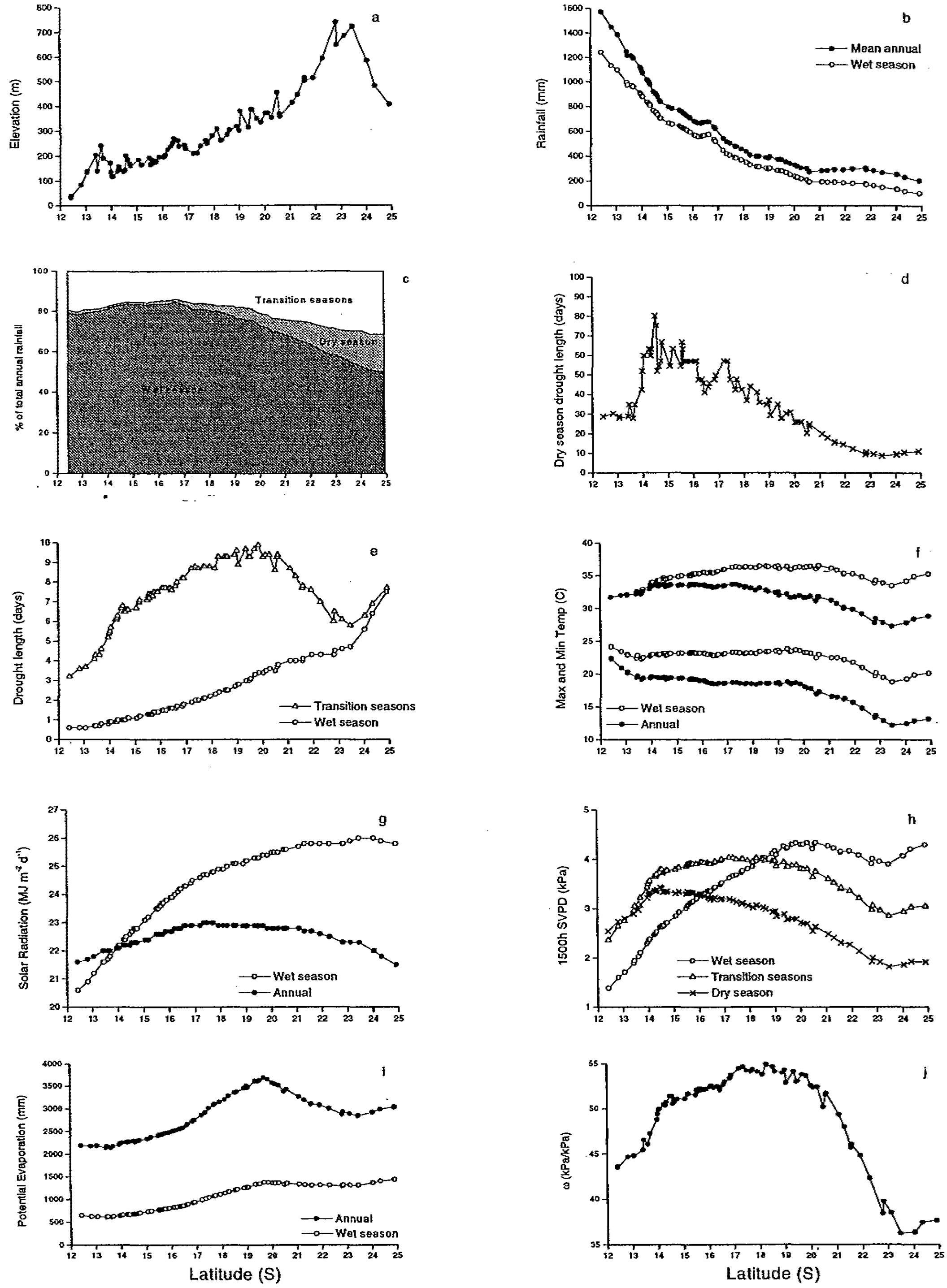
 a
Elevation (m)
b
Rainfall (mm)
Mean annual
Wet season
c
% of total annual rainfall
Transition seasons
Dry season
Wet season
d
Dry season drought length (days)
e
Drought length (days)
Transition seasons
Wet season
f
Max and Min Temp (C)
Wet season
Annual
g
Solar Radiation (MJ m-2 d-1)
Wet season
Annual
h
1500h SVPD (kPa)
Wet season
Transition seasons
Dry season
i
Potential Evaporation (mm)
Annual
Wet season
j
α (kPa/kPa)
Latitude (S)
Latitude (S)

Figure 6.1

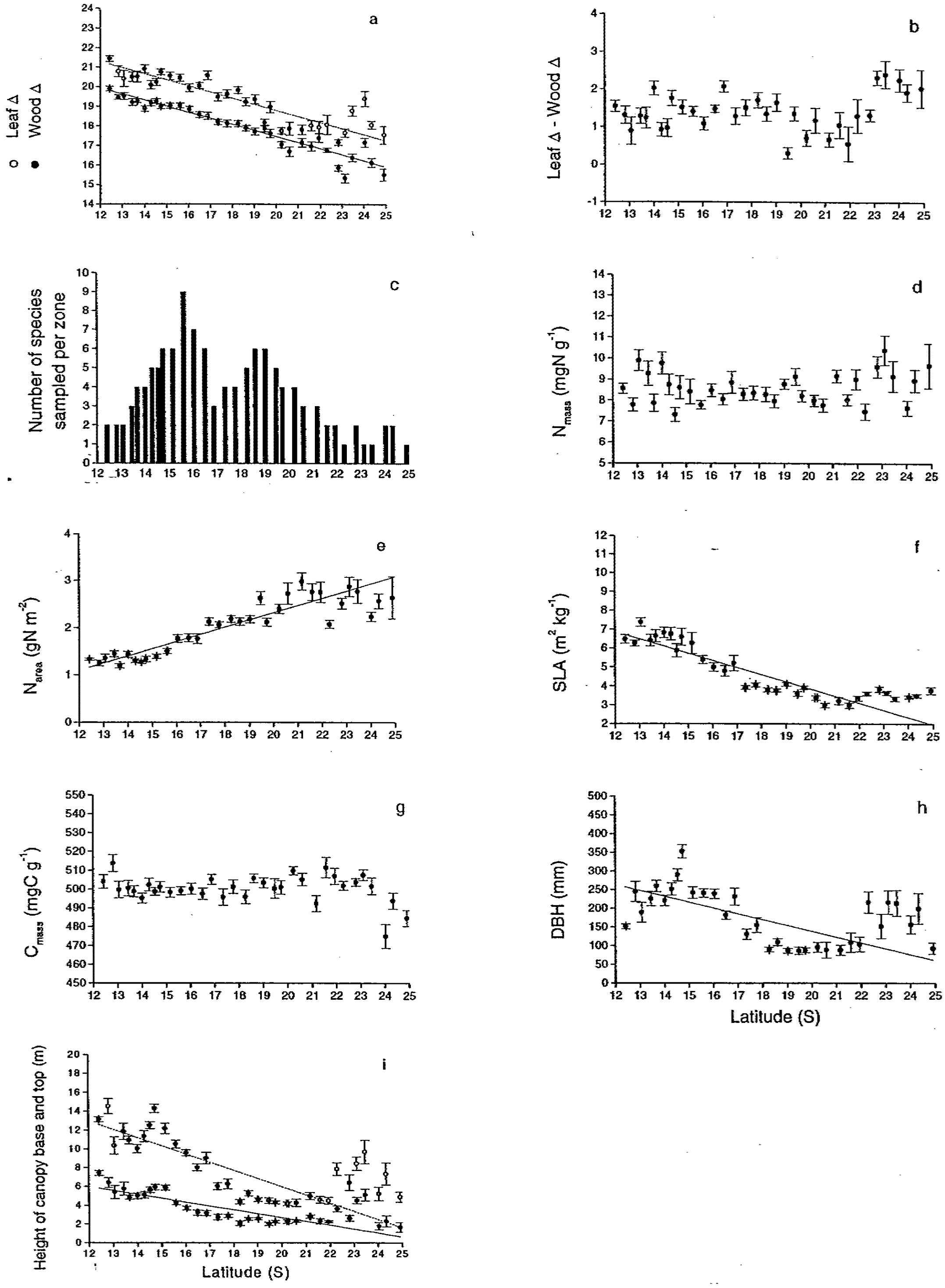

a
○ Leaf Δ
● Wood Δ
b
Leaf Δ - Wood Δ
c
Number of species sampled per zone
d
N_{mass} (mgN g^{-1})
e
N_{area} (gN m^{-2})
f
SLA (m^2 kg^{-1})
g
C_{mass} (mgC g^{-1})
h
DBH (mm)
Latitude (S)
i
Height of canopy base and top (m)
Latitude (S)

Figure 6.2

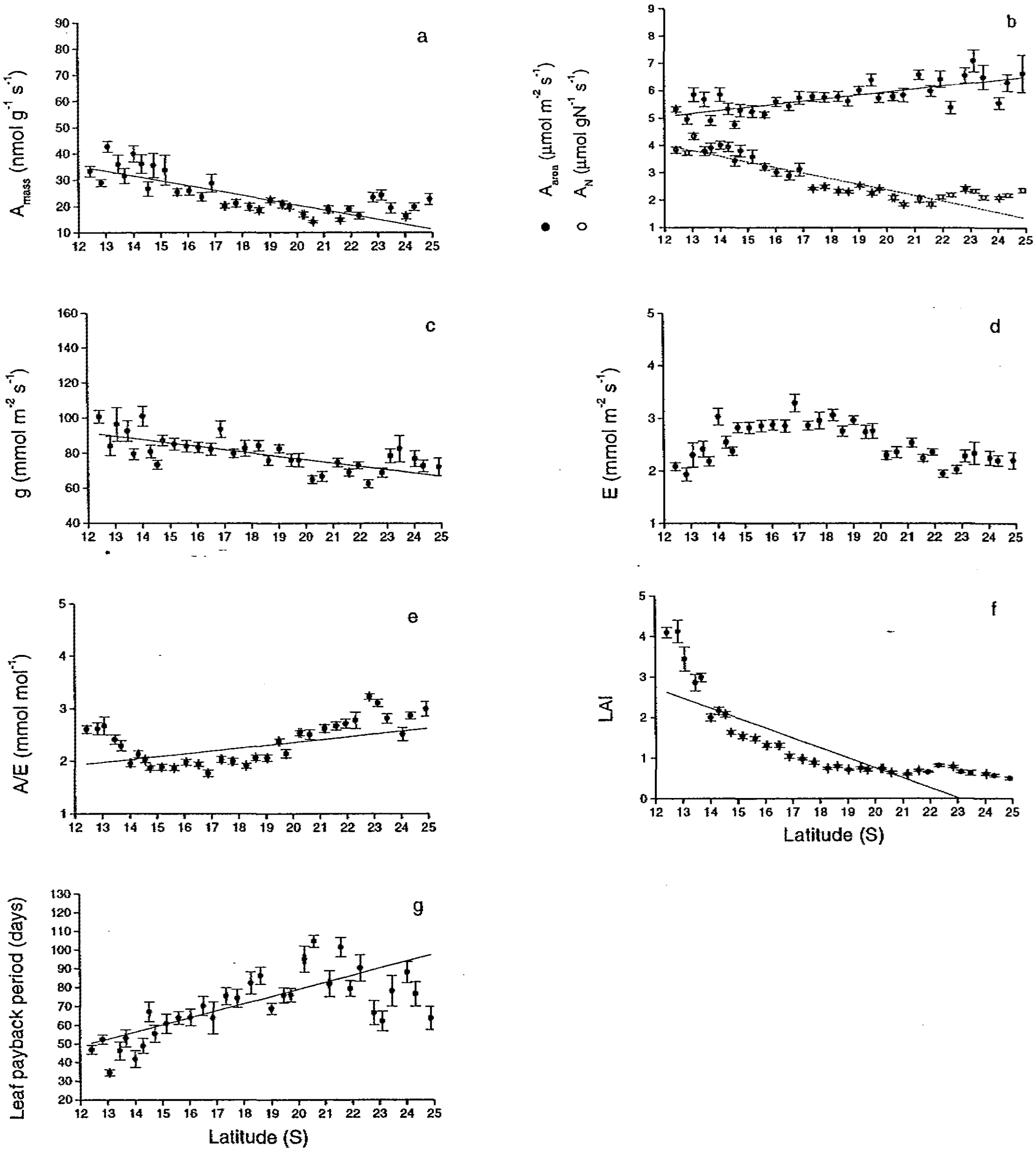
a
A_{mass} (nmol g^{-1} s^{-1})
90
80
70
60
50
40
30
20
10
12 13 14 15 16 17 18 19 20 21 22 23 24 25
b
● A_{area} (µmol m^{-2} s^{-1})
○ A_N (µmol gN^{-1} s^{-1})
9
8
7
6
5
4
3
2
1
12 13 14 15 16 17 18 19 20 21 22 23 24 25
c
g (mmol m^{-2} s^{-1})
160
140
120
100
80
60
40
12 13 14 15 16 17 18 19 20 21 22 23 24 25
d
E (mmol m^{-2} s^{-1})
5
4
3
2
1
12 13 14 15 16 17 18 19 20 21 22 23 24 25
e
A/E (mmol mol^{-1})
5
4
3
2
1
12 13 14 15 16 17 18 19 20 21 22 23 24 25
f
LAI
5
4
3
2
1
0
12 13 14 15 16 17 18 19 20 21 22 23 24 25
Latitude (S)
g
Leaf payback period (days)
130
120
110
100
90
80
70
60
50
40
30
20
12 13 14 15 16 17 18 19 20 21 22 23 24 25
Latitude (S)

Figure 6.3

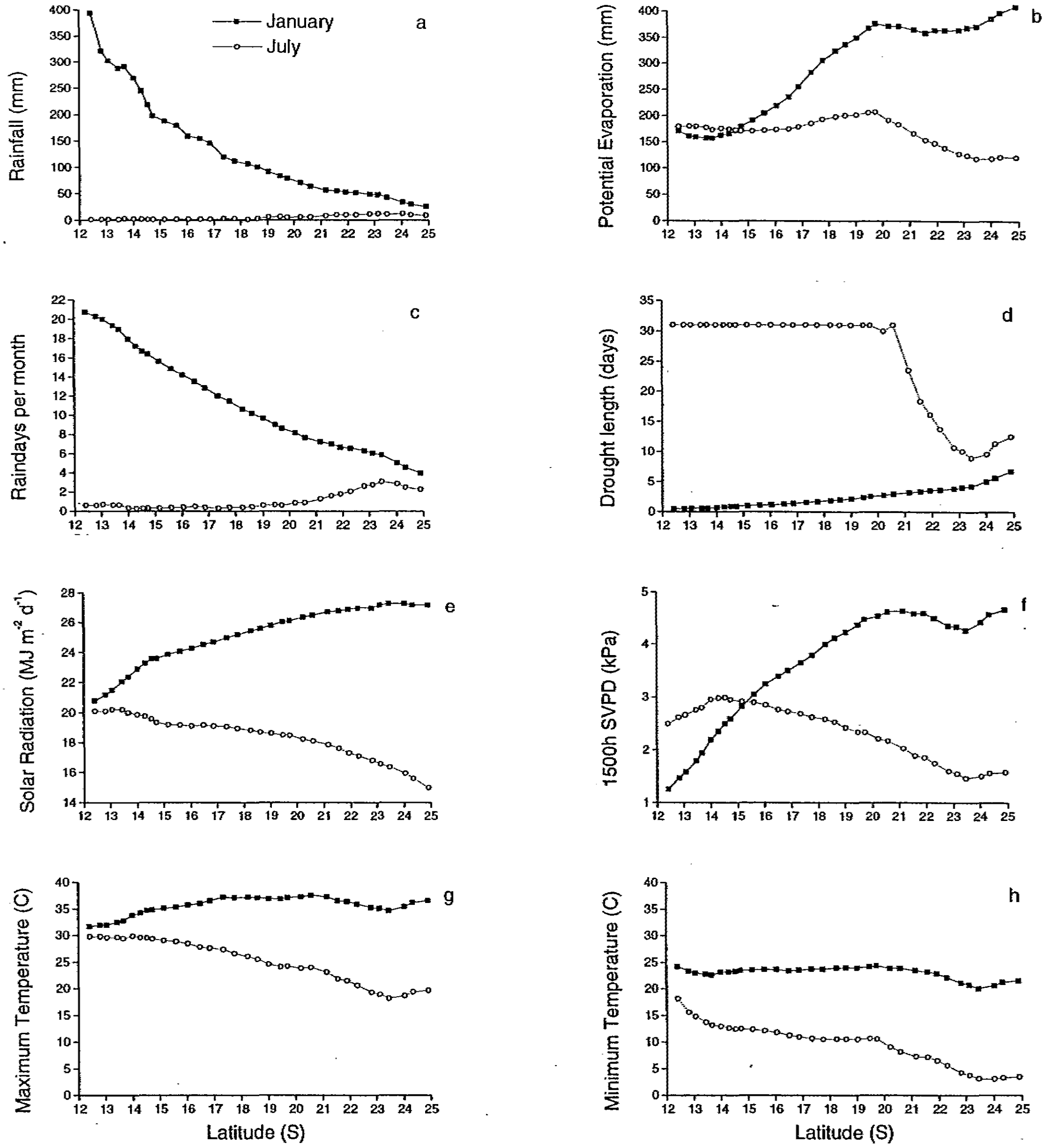
a
January
July
Rainfall (mm)
0
50
100
150
200
250
300
350
400
b
Potential Evaporation (mm)
c
Raindays per month
0
2
4
6
8
10
12
14
16
18
20
22
d
Drought length (days)
0
5
10
15
20
25
30
35
e
Solar Radiation (MJ m^{-2} d^{-1})
14
16
18
20
22
24
26
28
f
1500h SVPD (kPa)
1
2
3
4
5
g
Maximum Temperature (C)
h
Minimum Temperature (C)
0
5
10
15
20
25
30
35
40
12
13
14
15
16
17
18
19
20
21
22
23
24
25
Latitude (S)

Figure 6.4

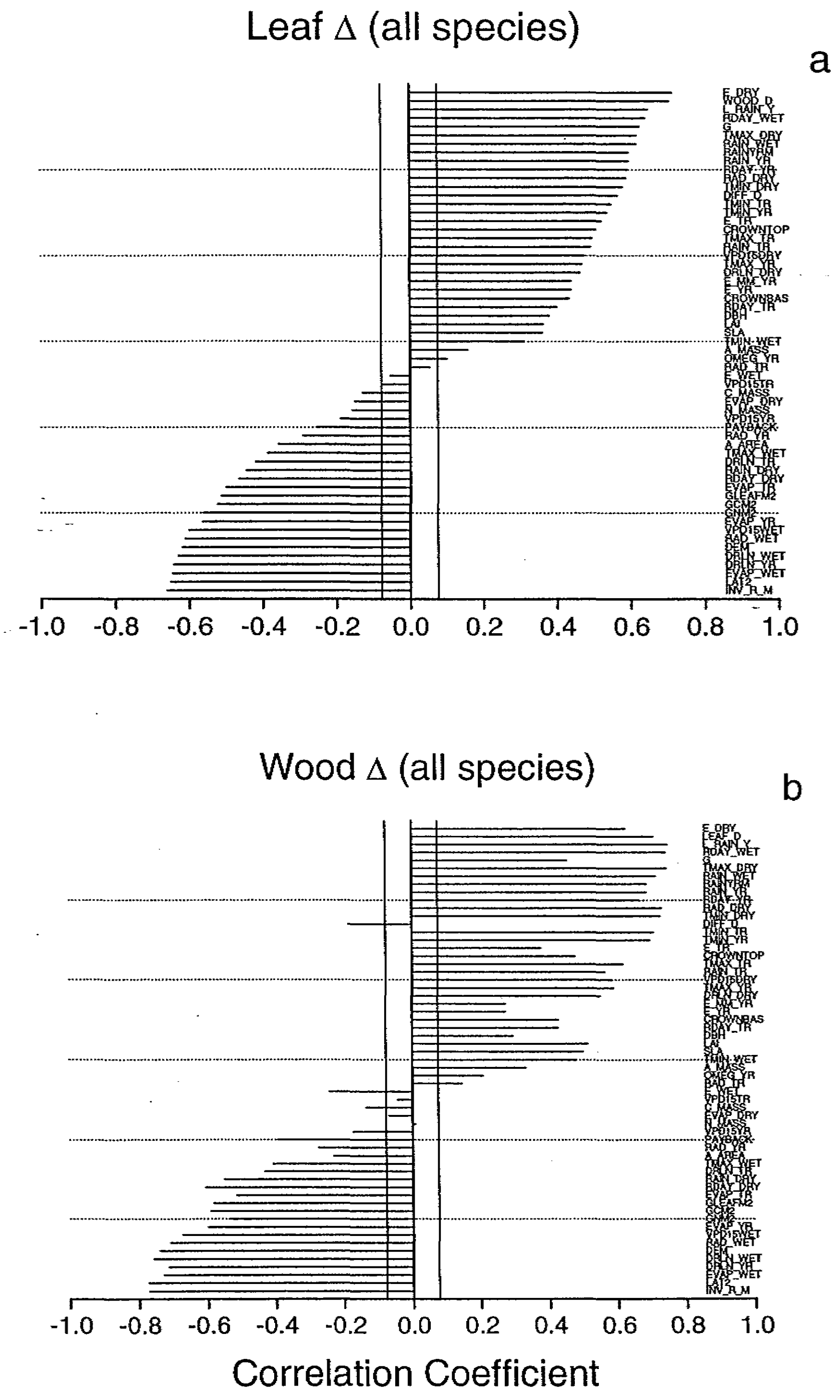

Leaf Δ (all species)
a
E_DRY
WOOD_D
L_RAIN_Y
RDAY_WET
G
TMAX_DRY
RAIN_WET
RAINYRM
RAIN_YR
RDAY_YR
RAD_DRY
TMIN_DRY
DIFF_D
TMIN_TR
TMIN_YR
E_TR
CROWNTOP
TMAX_TR
RAIN_TR
VPD15DRY
TMAX_YR
DRLN_DRY
E_MM_YR
E_YR
CROWNBAS
RDAY_TR
DBH
LAI
SLA
TMIN_WET
A_MASS
OMEG_YR
RAD_TR
E_WET
VPD15TR
C_MASS
EVAP_DRY
N_MASS
VPD15YR
PAYBACK
RAD_YR
A_AREA
TMAX_WET
DRLN_TR
RAIN_DRY
RDAY_DRY
EVAP_TR
GLEAFM2
GCM2
GNM2
EVAP_YR
VPD15WET
RAD_WET
DEM
DRLN_WET
DRLN_YR
EVAP_WET
LAI2
INV_R_M
-1.0
-0.8
-0.6
-0.4
-0.2
0.0
0.2
0.4
0.6
0.8
1.0
Wood Δ (all species)
b
E_DRY
LEAF_D
L_RAIN_Y
RDAY_WET
G
TMAX_DRY
RAIN_WET
RAINYRM
RAIN_YR
RDAY_YR
RAD_DRY
TMIN_DRY
DIFF_D
TMIN_TR
TMIN_YR
E_TR
CROWNTOP
TMAX_TR
RAIN_TR
VPD15DRY
TMAX_YR
DRLN_DRY
E_MM_YR
E_YR
CROWNBAS
RDAY_TR
DBH
LAI
SLA
TMIN_WET
A_MASS
OMEG_YR
RAD_TR
E_WET
VPD15TR
C_MASS
EVAP_DRY
N_MASS
VPD15YR
PAYBACK
RAD_YR
A_AREA
TMAX_WET
DRLN_TR
RAIN_DRY
RDAY_DRY
EVAP_TR
GLEAFM2
GCM2
GNM2
EVAP_YR
VPD15WET
RAD_WET
DEM
DRLN_WET
DRLN_YR
EVAP_WET
LAI2
INV_R_M
-1.0
-0.8
-0.6
-0.4
-0.2
0.0
0.2
0.4
0.6
0.8
1.0
Correlation Coefficient

Figure 6.5

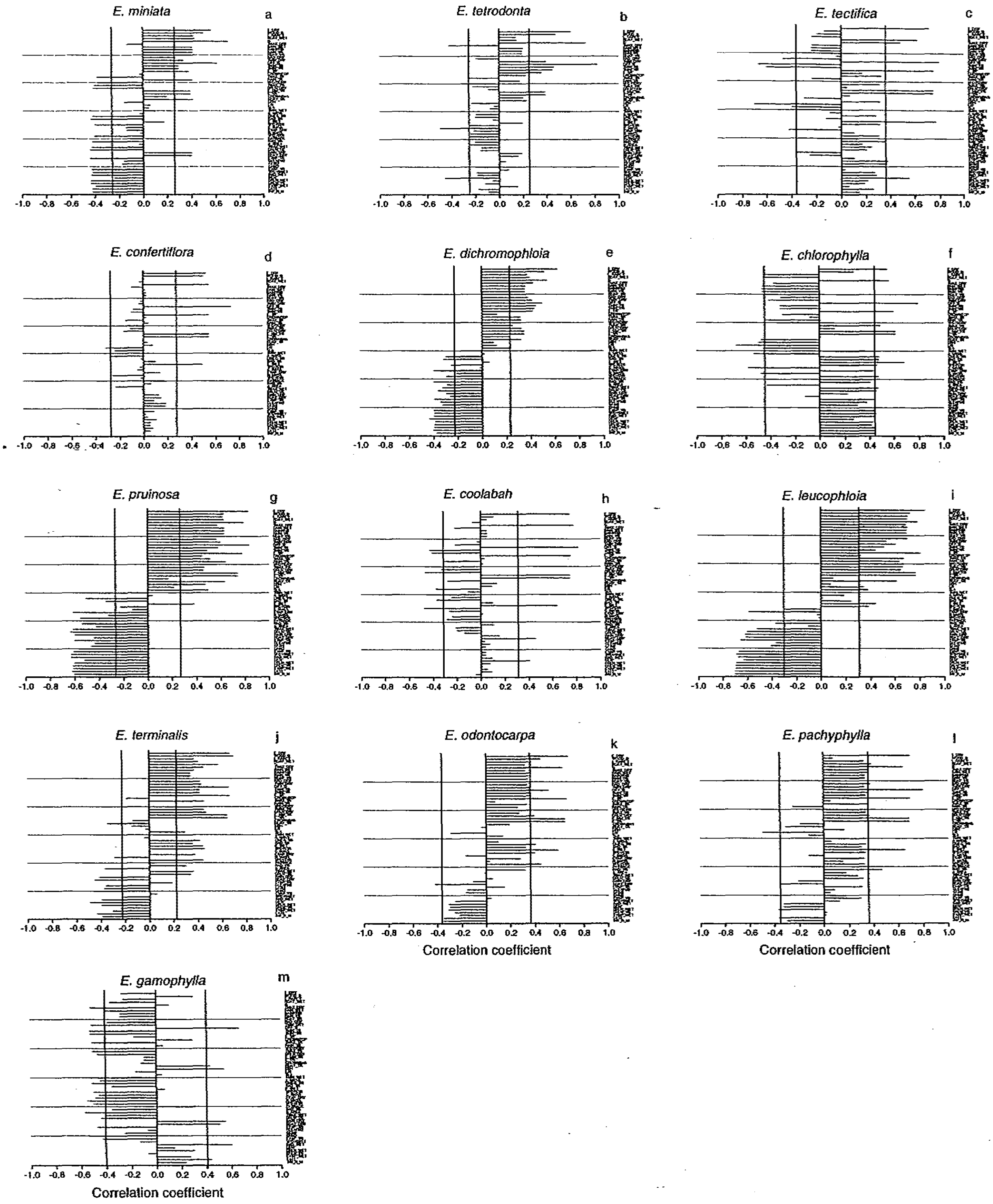

E. miniata
a
E. tetrodonta
b
E. tectifica
c
E. confertiflora
d
E. dichromophloia
e
E. chlorophylla
f
E. pruinosa
g
E. coolabah
h
E. leucophloia
i
E. terminalis
j
E. odontocarpa
k
E. pachyphylla
l
E. gamophylla
m
-1.0 -0.8 -0.6 -0.4 -0.2 0.0 0.2 0.4 0.6 0.8 1.0
Correlation coefficient

Figure 6.6

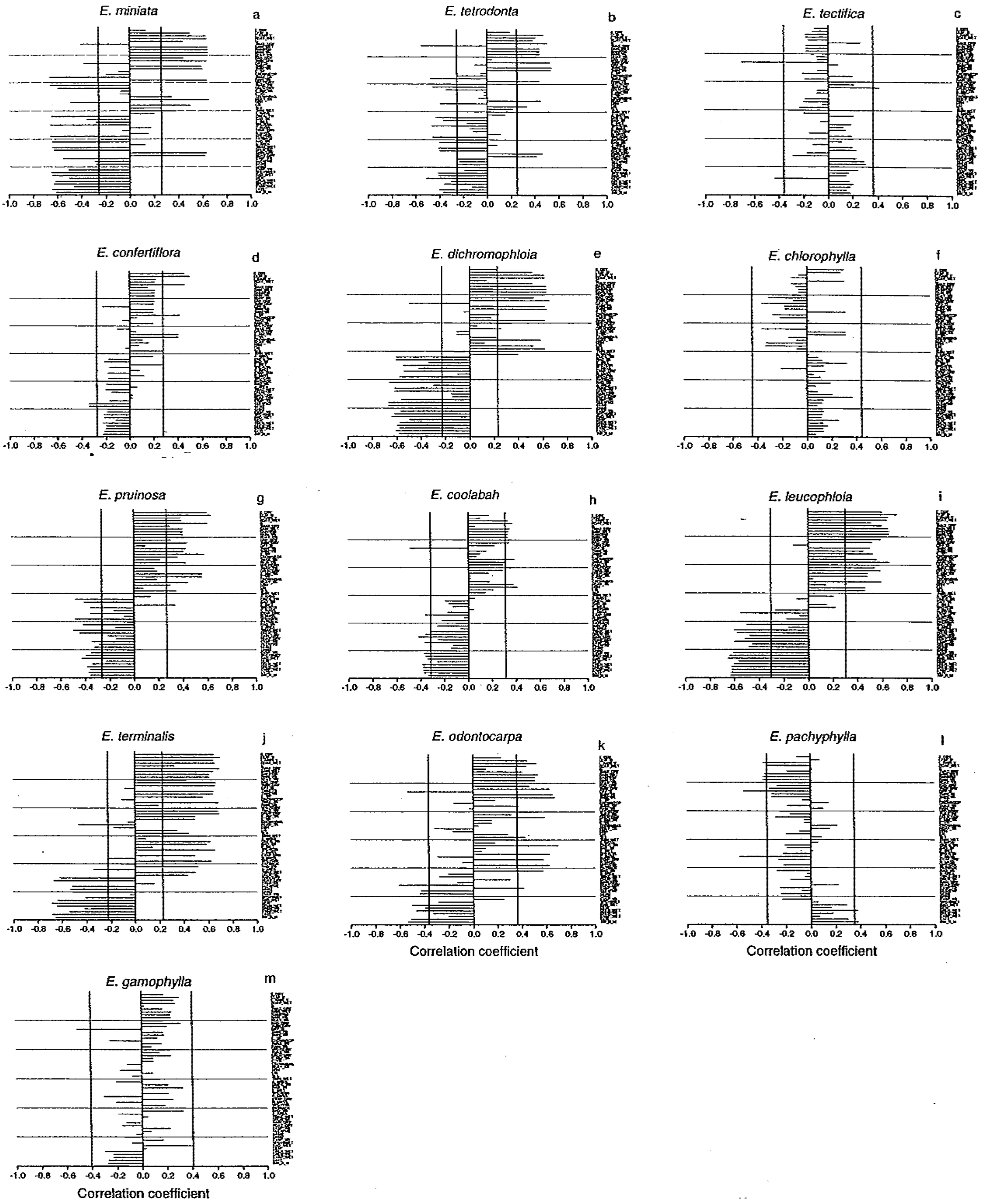

E. miniata
a
E. tetrodonta
b
E. tectifica
c
E. confertiflora
d
E. dichromophloia
e
E. chlorophylla
f
E. pruinosa
g
E. coolabah
h
E. leucophloia
i
E. terminalis
j
E. odontocarpa
k
E. pachyphylla
l
E. gamophylla
m
-1.0 -0.8 -0.6 -0.4 -0.2 0.0 0.2 0.4 0.6 0.8 1.0
Correlation coefficient

Figure 6.7

Chapter 7

Plasticity of carbon isotope discrimination and other characteristics in *Eucalyptus* species along an environmental gradient in the Northern Territory, Australia

Summary

1. Plasticity of morphological and physiological characteristics is thought to provide a competitive advantage under conditions of high resources, but may be disadvantageous under conditions of low resources.

2. The ability of a series of dominant *Eucalyptus* species to alter a suite of physiological and morphological characteristics was investigated along a complex environmental gradient marked by an 8-fold decrease in total annual rainfall.

3. The species which showed the greatest changes in the values of plant characters had the widest distributions. The size of the distribution of a species did not depend upon location along the transect.

4. The elasticity of most characters did not depend on either the location of the species along the transect or the size of the distribution of the species along the transect.

5. There were no trends in the coefficients of variation of the measured plant characters across the distribution of the species in most cases. Increasing levels of stress did not seem to be strongly selecting for a single optimal solution.

6. Physiological parameters, specifically wood and leaf Δ, had lower elasticities than the morphological parameters, emphasizing that subtle changes in Δ are of potentially great importance as indicators of plant performance.

7.1 Introduction

> "The evolutionary response to insufficient resources is to fix genetically the patterns of allocation that maximize acquisition of the limiting resource and to reduce overall resource requirements by reducing growth rate" (Chapin 1991).

Plants that are native to low resource environments have often been found to have inherently low growth rates, even when transplanted to resource rich environments (Lambers & Poorter 1992). This conservative behavior may limit the competitive ability of the species in resource rich environments, such that their distributions in resource poor environments represent refugia. Alternatively, conservative behavior in a low resource environment may be a positive adaptation since low resource environments are also usually highly variable environments, when variability is expressed in terms relating to the mean conditions (Ehleringer 1993). Conservative behavior would prevent an individual from responding to an isolated increase in resource levels, such as an isolated intense rain event, as if such abundance were the norm (Crick & Grime 1987). Where resources normally dictate limited vegetative growth, and therefore a limited, but reliable reproductive effort, responding to a temporary increase in resources with luxurious vegetative growth would only be viable when there is some surety the resource supply will last long enough for reproduction to occur. Maintaining the ability to respond to variable conditions probably involves some level of cost to the plant, which if rarely called upon could drop out of a population (Scheiner 1993). Foraging for resources in either space or time is linked to plasticity as it involves the expenditure of capital reserves in order to discover pockets of resources and gambles on the rate of return (Hutchings & de Kroon 1994).

A hypothetical resource gradient could therefore see several different successful growth strategies, depending on the amounts and probability distributions of those resources. Along a rainfall gradient one would expect intense competition for another resource, such as light, where water was not limiting. As resources decrease, or become more seasonal, the evergreen tree growth form may be replaced by strategies with very high growth rates of low investment and consequently short life span tissue. The seasonally deciduous or annual growth strategy works where resources are intermittent, but sufficient for completion of the complete life-cycle. With further reduction in both availability and reliability of resources only the genetically controlled conservative behavior becomes viable.

The rate of water-use relative to carbon gain per unit leaf-area would be a key indicator of the growth strategy of a plant along a rainfall gradient. Other key characters would be the canopy leaf area index and the investment into the leaf of carbon and nitrogen per unit area. The dynamics of the changing efficiency of the exchange of water for carbon with increasing conductance, with the trade-off being increasing LAI, rather than the rates of an individual leaf, are complex. Increasing leaf area index brings the penalty of decreasing average light levels within the canopy. The levels of nitrogen investment determining photosynthetic capacities may then determine the levels of carbon investment necessary to reduce herbivory, just as the levels of water stress may determine the need for carbon investment for mechanical strength. Besides the light environment aspects, LAI is constrained by the influences on the leaf payback period.

Determining the expected changes in these characters from a theoretical analysis optimizing their costs and benefits is beyond the scope of this Chapter. What is of interest is the scale of the change of these characters across the distribution of a series of species along a resource gradient. In using naturally occurring populations, the expression of the potential genetic plasticity is limited to that which is actually functionally successful. The changes in the characters of co-occurring species, and replacement species, at a series of points across the distribution of the species reflect a series of "common gardens" with changing resource levels. Since the growth conditions are "appropriate" for the species, i.e. arid species are not growing in a glasshouse with daily watering and nutrient supplementation, the range of the responses of the characters should provide more information as to their dynamics than would occur by forcing growth under artificial conditions.

The scale of the changes in plant characters across a resource gradient may determine where along the gradient the species naturally occurs and the range of conditions over with it occurs. The absolute magnitude of tolerable variation may be important, or the relativized shifts measured by "elasticities" (as described in Chapter 4) may be important. Unitless elasticities, measuring a percentage change in a dependent variable in response to a percentage change in an independent variable, allow comparisons between characters and inferences as to whether physiological or morphological characters are more plastic, and which characters are determining plant performance.

Besides the shifts in the mean values of characters between and within species across the gradient, there may be changes in variability in characters at population level. Increasing stress levels may reduce variability toward a single successful strategy for key characters. However, decreasing mean resource levels also tend to correspond to increasing variability in resource levels, and co-existing sub-populations with alternative, but equally successful strategies may develop as has been reported in some desert species (Ehleringer 1993).

The goals of this Chapter were to analyze variability in the available physiological and morphological plant characters in relation to the location of the distribution of the species along the gradient, and the size of the range of the distribution of the species. It was hypothesized that:

1. At the wetter end of the transect, plants will have wide distributions, while at the drier end of the transect adaptions will be more critical and distributions will be narrower.
2. Wide distributional ranges will require the ability to make large changes in critical characters, but the rate of change of characters per unit change in resource should be higher under low resources.
3. Morphological characters, such as leaf area index, will be more plastic (measured as absolute changes as well as elasticities) than physiological characters, such as Δ.

4. The coefficients of variation of key characters will increase with decreasing mean resource levels, since the decreasing mean corresponds to increasing variation in those resource levels.

7.2 Methods

The field and laboratory methods used to sample leaf and wood Δ, leaf mass per unit area (LMA), and leaf nitrogen and carbon contents (N_{mass}, N_{area}, C_{mass}, and C_{area}) were described in Chapter 3. The monthly mean climatic data was generated by ANUCLIM 1.8 (Centre for Resource and Environmental Studies, ANU) as described in Chapter 3. Photosynthetic capacities, leaf conductances, transpiration rates, and leaf payback periods were calculated as described in Chapter 5. The collection of other morphological characters was described in Chapter 6. The elasticities were calculated using Equation 4.7, i.e.

$$\varepsilon_{XY} = \frac{\partial X}{\partial Y}\frac{Y}{X} \qquad \text{Eq. 7.1}$$

in response to changes in latitude because latitude was the parameter most linearly related to Δ (see Chapter 6). Statistical analyses were made using SAS (6.12: SAS Institute Inc.), SYSTAT (9.01: SPSS Inc,), and Microcal Origin 5.0.

7.3 Results

A one-way ANOVA of the species distributions followed by a Student-Newman-Keuls multiple range test grouped the 13 species sampled into 6 groups; those with distributional means north of 14°S (*E. miniata*, *E. tetrodonta*, and *E. tectifica*), those with mean distributions within 15°S (*E. confertiflora*, *E. chlorophylla*), within 16°S (*E. dichromophloia*), within 17 to 18°S (*E. coolabah*, *E. pruinosa* and *E. leucophloia*), those between 19 and 20°S (*E. odontocarpa*, *E. terminalis*, and *E. pachyphylla*), and *E. gamophylla* with a distributional mean of 23½°S (Table 7.1). The range of *E. coolabah* was significantly different from that of *E. leucophloia*, as were the ranges of *E. odontocarpa* and *E. pachyphylla*.

The mean values for each species of most of the measured and calculated parameters were correlated with the distributional means (Figures 7.1 and 7.2). The species mean Δ of both the leaf and wood samples was closely related to the location of the species on the transect (Figures 7.1a and 7.1b). The species mean differences between the leaf and wood Δ values were unrelated to the location along the transect of the species (Figure 7.1c). Only *E. pachyphylla* was clearly distinguishable from the other species which had broad overlapping ranges of non-significant differences (SNK test). The species mean leaf mass per unit area, the leaf carbon content per unit area, and the leaf nitrogen content per unit area were all related to the location of the species along the transect, with values increasing towards the drier south (Figures 7.1d, 7.1e, 7.1f). The species mean mass-based leaf chemistry parameters (N_{mass} and C_{mass}) were not related to the species position along the transect (Figures 7.1g and 7.1h). At the species level, the size of the sampled trees decreased from north to south as measured by both the trunk diameters and heights (Figures 7.1i and 7.1j). *E. tetrodonta* was significantly taller than *E. miniata* and *E. chlorophylla*. *E. tectifica*, *E. confertiflora*, and *E. dichromophloia* were not significantly different in height, and the rest of the species, except the mallee shrubs (*E. gamophylla*, *E. odontocarpa*, and *E. pachyphylla*) which were significantly shorter, did not significantly differ in height.

The semi-deciduous species, *E. confertiflora*, had significantly higher calculated A_{mass} values than the other species (Figure 7.2a). *E. miniata* and *E. tectifica* were the next highest species, and all of the other species showed little differences in calculated A_{mass}. The species mean A_{mass} values were related to the position of the species along the transect (at $\alpha = 0.051$) as were the species mean calculated A_{area} and calculated g values (Figures 7.2b and 7.2c). The species mean calculated transpiration rates did not depend upon the location of the species along the transect (Figure 7.2d). *E. pruinosa*, *E. chlorophylla*, and *E. coolabah*, which had distributions in the middle of the transect were the SVPD values were highest, had the next highest calculated E values, while *E. odontocarpa*, *E. gamophylla*, and *E. tetrodonta* had low values distinguishable from the other species. The species mean instantaneous water-use efficiencies increased from north to south depending on the location of the species along the transect (Figure 7.2e). *E. gamophylla* had significantly higher calculated A_{area}/E ratios than the other species which were harder to distinguish into groups. The ratio of the total annual rainfall to the species mean total annual transpiration gives an upper boundary for leaf area index. The low calculated E of *E. tetrodonta* in the wet northern part of the transect gave it the highest potential LAI (Figure 7.2f). The potential LAI values of *E. tectifica* and *E. miniata*, and *E. confertiflora* and *E. dichromophloia* were distinguishable pairs from the rest of the species. The ratio of the carbon content of the leaves to the calculated assimilation rate (both on a mass-basis) gives an estimate of the period required for the leaf to become an exporter of carbon (ignoring translocation that might occur at senescence). The species mean leaf payback period was related to the position of the species along the transect (Figure 7.2g). The deciduous *E. confertiflora* had a significantly shorter payback period than the other species. *E. dichromophloia* and *E. odontocarpa*, and lastly *E. pachyphylla* had significantly longer payback periods.

The plasticity (here meaning the change in the value of a parameter from north to south across the distribution of a species as predicted from the end points of the linear regressions of the data against latitude) in leaf and wood Δ, LMA, N_{area}, and N_{mass} were linked to size of the distributional range of the species, but not to the position of the species along the transect (Figure 7.3). Leaf Δ increased in several species with ranges less than 4° latitude, and decreased in all species with greater ranges (Figure 7.3b). The patterns of change in leaf Δ were completely independent of position along the transect (Figure 7.3a). The sensitivity of the responses of leaf Δ (change in leaf Δ per degree latitude) of *E. tectifica* and *E. chlorophylla* were higher than those in the other species.

The changes in wood Δ values across the distributions of each species were not as extreme as the changes in leaf Δ values (Figure 7.3c). Again some species with narrower distributions (less than 3 ° latitude) showed slight increases in wood Δ values, but those species with wider distributions showed changes in wood Δ up to -2.2‰ (Figure 7.3d). There was no relationship between the plasticity of wood Δ values and position of the species along the transect.

Species with wider distributional ranges had larger changes in leaf mass per unit area (Figure 7.3f). Except for *E. pachyphylla*, all of the species showed patterns of increasing LMA from north to south across their distributions. The magnitude of the changes in LMA did not depend on the location of the species along the transect (Figure 7.3e).

The magnitude of the changes in leaf nitrogen contents on both an area- and mass-basis did not depend upon the location of the species along the transect, but were related to the size of the distribution of the species (Figures 7.3g, 7.3h, 7.3i, and 7.3j). The changes in N_{area} reflect the changes in LMA except in the northernmost species which had increases in LMA across their distributions without changes in N_{area} and therefore decreases in N_{mass}. The changes in N_{mass} were greatest in species with narrow distributions occurring in the northern part of the transect. The species with distributional midpoints south of around 16 °S showed little change in N_{mass} across their distributions while those to the north had decreasing N_{mass} values resulting in a significant relationship between N_{mass} and distributional range, and N_{mass} and distributional midpoint. The changes in N_{mass} of most species were less than ± 0.5 mgN g^{-1} °Lat^{-1}, except for *E. tectifica* and *E. chlorophylla* which changed -2.3 mgN g^{-1} °Lat^{-1}.

The patterns in C_{area} followed the patterns of LMA, while the changes in the C_{mass} values were neither related to the location of the species nor the range size of the species (Figures 7.3k and 7.3l). The changes in the sizes of the sampled trees did not depend on the location of the species along the transect nor on the distributional range of the species (Figures 7.3m, 7.3n, 7.3o, and 7.3p)

The patterns in the area- and mass-based leaf nitrogen contents were reflected in the patterns of the calculated area- and mass-based photosynthetic capacities. A_{mass} decreased across the distributions of most species (from north to south), with the greatest decreases in the north of the transect (Figure 7.4a). Although the changes in

A_{mass} were related to the location of the species along the transect they were not related to the distributional range of the species (Figure 7.4b).

The plasticity in the calculated A_{area} related to both the position along the transect of the species ($\alpha = 0.058$), and to its distributional range (Figures 7.4c and 7.4d). Species with narrower distributions in the north showed declining calculated A_{area} across their distributions, while species with wider distributions (and in the middle of the transect) had increases in calculated A_{area}.

Most species exhibited decreases in calculated g across their distribution, but neither the magnitude nor sensitivity of this reduction was related to either the distributional range of the species or the distributional midpoint (Figures 7.4e and 7.4f). Since the SVPD values tended to increase from the northern end to the middle of the transect, and then decrease on towards the south, the species in the northern half of the transect had increasing values of calculated E across their distributions, while the species in the south had decreasing values of calculated E (Figure 7.4g). The magnitude of the changes of the calculated E did not depend on the size of the distribution of the species (Figure 7.4h)

Unlike the plasticity in leaf Δ which was related to the size of the distribution of the species, the changes in the ratio of the calculated A_{area} to the calculated E were not related to either the position of the species on the transect or the size of the distribution of the species along the transect (Figures 7.4i and 7.4j).

The largest changes in rainfall occurred in the northern part of the transect, and therefore the largest changes in the calculated potential maximum *LAI* occurred in the species in the northern part of the transect (Figure 7.4k). All of the species were predicted to show decreases in *LAI* across their distributions, and although the size of the decrease depended upon the location of the species along the transect it did not depend upon the size of the distribution of the species (Figure 7.4l).

The changes in the time required to recover the construction costs of a leaf where highest across the distributions of the northern species (Figure 7.4m). The changes in the payback period were unrelated to the size of the distribution ranges of the species (Figure 7.4n). The change in payback period per degree of latitude was highest in the northern species, with *E. tectifica* and *E. chlorophylla* having the highest values.

The unitless elasticities, measuring the percent change in a dependant variable to a one percent change in an independent variable, capture the sensitivities of the responses and allow comparisons to be made between parameters with different magnitudes. C_{mass}, wood Δ, followed by leaf Δ, had the lowest elasticities of the measured and calculated parameters. A one percent movement from north to south across the distribution of each of the species caused a shift in leaf Δ of between -0.5 and 0.7%. The wood Δ values responded between -0.8 and 0.2% to a similar change in location. The elasticities of both the leaf and wood Δ of the species were unrelated to the location of the species along the transect or the size of the distribution of the species along the transect (Figures 7.5a, 7.5b, 7.5c, and 7.5d) .

The elasticities of LMA were all positive, except for *E. pachyphylla*. The elasticity of the LMA of a species was related to the location of the species along the transect ($\alpha = 0.07$), but not to the size of the distribution of the species (Figure 7.5e and 7.5f). The elasticities of N_{area} were not related to the location of the species along the transect, but were related to the size of the distribution of the species ($\alpha = 0.07$) (Figures 7.5g and 7.5h), while to opposite was true about the elasticities of C_{area}. The elasticities of C_{area} were correlated with the location of the species along the transect, but not the size of the distribution of the species (Figures 7.5i and 7.5j).

The elasticities of the species N_{mass} were related to both the location of the species along the transect and the size of the distribution of the species (Figures 7.5k and 7.5l). The correlations were the result of the behaviors of the three northernmost species, *E. miniata*, *E. tetrodonta*, and *E. confertiflora*, as the other species showed much less range in their elasticities.

The elasticities of C_{mass} and the two measures of tree size, DBH and height, were all unrelated to either species location or size of distribution (Figures 7.5m, 7.5n, 7.5o, 7.5p, 7.5q, and 7.5r). The range in the elasticities of DBH (between -6.0 and 4.7%) and height (between -3.8 and 4.2%) was the largest of all of the measured parameters.

Of the calculated parameters, the elasticities of calculated A_{mass} had the largest range (between -8.6 and 1.1%). The elasticities of species A_{mass} were related to the location of the species along the transect ($\alpha = 0.06$), but not to the size of the distribution of the species (Figures 7.6a and 7.6b). The elasticities of *E. tectifica* and *E.*

chlorophylla were lower than those of the other species which increased from north to south across the transect.

The elasticities of calculated A_{area} were related to both the location of the species along the transect ($\alpha = 0.06$) and the size of the distribution of the species along the transect (Figures 7.6c and 7.6d). The elasticities of *E. tectifica* and *E. chlorophylla* were again lower than those of the other species.

The elasticities of calculated g were unrelated to either the location or distributional size of the species along the transect (Figures 7.6e and 7.6f). Because of the pattern of the SVPD across the transect, the elasticities of the calculated E of the northern species were positive, while those of the southern species were negative (Figure 7.6g). The elasticities of calculated E were unrelated to the size of the distribution of the species along the transect (Figure 7.6h).

The elasticities of the ratio of calculated A_{area} to calculated E of the species increased from north to south across the transect, and with the increasing size of the distribution of the species along the transect ($\alpha = 0.06$) (Figures 7.6i and 7.6j). *E. tectifica*, *E. chlorophylla*, and *E. gamophylla* were all below the general relationship of the elasticities of the other species and their location along the transect.

The elasticities of the calculated potential maximum *LAI* and the leaf payback period were both related to the location of the species along the transect, but not to the size of the distribution of the species (Figures 7.6k, 7.6l, 7.6m, and 7.6n). The elasticities of the calculated leaf payback periods of *E. tectifica* and *E. chlorophylla* were higher than those of the other species.

The elasticities of the parameters based on changes in total annual rainfall were all smaller than those based on changes in location (Figures 7.7 and 7.8). This was due to there being an eight-fold change in rainfall across the gradient while there was only a doubling in the latitude. The elasticities of the species calculated E, A_{area}/E, and *LAI* were correlated with the mean rainfall within the distribution of the species, and the elasticities of C_{mass} were correlated with the range in rainfall across the distribution of the species.

The coefficients of variation for the values within a zone for most of the measured and calculated parameters for most species did not exhibit trends across the distribution of the species. The coefficients of variation of N_{mass}, A_{mass}, A_{area}, and leaf payback period all increased (with α between 0.04 and 0.07) with increasing latitude (towards the south) in *E. miniata* (Figure 7.9). In *E. tetrodonta* the CV's of C_{mass} and the ratio of A to E (at $\alpha = 0.067$) both decreased across the distribution of the species (Figure 7.10). The CV of the wood Δ increased across the distribution of *E. confertiflora* from north to south (Figure 7.12). In *E. dichromophloia* the CV's increased in the tree heights and the wood Δ and decreased in the SLA, LMA, C_{area} and A_N values from north to south (Figure 7.13). In *E. pruinosa* the CV's of the height of the trees increased (Figure 7.15), and in *E. terminalis* the CV's of SLA, LMA, C_{area}, A_N, and the ratio of A to E all decreased from north to south (Figure 7.18). Of the mallee shrubs, the CV's of the LAI of *E. odontocarpa* increased (Figure 7.19), and the CV's of the tree height, leaf Δ, the ratio of A to E, the LAI, and c_i of *E. pachyphylla* all decreased (with α up to 0.06) (Figure 7.20). None of the coefficients of variation of any of the parameters of the remaining species (*E. tectifica*, *E. chlorophylla*, *E. coolabah*, *E. leucophloia*, and *E. gamophylla*) showed any significant trends across the distributions of the species (Figures 7.11, 7.14, 7.16, 7.17, and 7.21).

7.4 Discussion

The environment can probably influence the species mean value of a character independently from the plasticity of that character in response to environmental changes, as well as the variability of that character within a population (Scheiner 1993). However, the issues are clearly related as high rates of mortality at the unsuccessful extreme of the expression of a character would influence the population mean and probably the population variability, as well as possibly reducing the plasticity. Species experiencing high levels of competition in productive environments should respond to environmental heterogeneity primarily through morphological plasticity, while species occurring in relatively unproductive environments should respond to environmental heterogeneity via physiological plasticity (Grime, Crick & Rincon 1986). Phenotypic plasticity should be high for characters that are adaptations to environmental conditions the are likely to change many times during the lifespan of an organism, while genetic differentiation is predicted for characters that are likely to remain fairly constant during the lifespan of the organism (Bradshaw 1965).

From north to south along the transect in this study, there was a complex environmental gradient that was predominantly marked by an 8-fold decrease in total annual rainfall. Other factors affecting the water economies of plants also changed, and there was a general increase in the evaporative demands as well as an increase in the time between rain events.

The sampled dominant overstory *Eucalyptus* species segregated along the gradient according to most of the measured parameters. Species mean leaf and wood Δ, as well as tree size, decreased with increasing latitude (equivalent to decreasing total annual rainfall, increasing SVPD, and drought lengths), while leaf mass per unit area and area-based leaf nitrogen and carbon contents increased. The species mean calculated area-based photosynthetic capacities increased with latitude while calculated leaf conductances decreased. The species calculated potential maximum leaf area indices decreased with increasing latitude, while the calculated time required for the assimilation capacity to recover the carbon content of the leaves increased.

The large changes in the payback periods of the northern species may indicate the carbon return per unit leaf area was very high at the northern edge of the species distributions, and that much lower returns would still allow the leaf to have a positive contribution to the carbon balance of the tree. In contrast, in the south, the leaves may just be recovering their costs and may be unable to extend the payback period. However, the sensitivity of the northern species would indicate their inability to expand southwards.

Species replacements were usually not marked by obvious step-changes in any measured parameter. Across the distribution of a species, the characters changed such that species at the southern edges of their distributions had similar values to the replacement species at the northern edge of their distributions. Species distributions therefore seemed to be marked by reaching a limit in the ability to vary a parameter, while the magnitude of the parameter was not markedly different from that in the replacement species.

The size of the distribution of the species was linked to the size of the absolute change in the leaf and wood Δ, LMA, and leaf nitrogen concentrations. The range size of a species, and the ability to vary the value of a parameter did not depend upon the location of the species along the transect. As stress levels increased there did not seem to be increased specialization by the species which might have been reflected in narrower ranges or narrower physiological responses. The elasticities of most of the measured and calculated parameters did not depend on either the location of the species along the transect or the size of the distribution of the species along the transect.

The small sample size (of only 5 replicates per species per zone) may have made finding changes in the coefficients of variation of characters across the distribution of the species difficult. There were no clear trends in most of the CV's of most of the characters in all of the species. The two cases where the CV of the wood Δ of a species significantly increased ($\alpha = 0.05$) with increasing latitude could reflect the presence of specialized sub-populations as was found in *Encelia farinosa* (Ehleringer 1993). However, neither *E. confertiflora* nor *E. dichromophloia* were found in the southernmost areas where the variability in rainfall was the highest. Where low rainfall also correlates with high inter-annual variability Ehleringer (1993) proposed that parts of the population of could specialize for the good years and be able to be very productive (and reproductive) in these isolated events, while the rest of the population maintained a conservative strategy which was more successful in the average conditions with low, but consistent reproduction.

Since all the trees in this study were not growing in a common environment it was not possible to separate the genetic and environmental components of the observed patterns of plasticity. Along an altitudinal gradient in Hawaii *Meterosideros polymorpha* exhibited genetically constrained morphological changes and environmentally constrained physiological changes (Cordell et al. 1998). Scots pine (*Pinus sylvestris*) at a series of sites across exhibited structural changes rather than changes in water-use characteristics under a range of climatic conditions (Palmroth et al. 1999).

The elasticities of the species mass-based leaf carbon content, followed by the wood Δ and then the leaf Δ were the lowest of the measured parameters. The morphological characters, especially the measures of tree size, had the highest elasticities. The lack of plasticity in Δ has led to it being referred to as a "set point" (Ehleringer 1993), which the plant attempts to maintain by altering the physiological and morphological characters which affect it. The lack of plasticity in Δ means that subtle changes are of potentially great importance as indicators of plant performance. Characters which were strongly correlated with fitness have shown the least plasticity of measured parameters in other studies (Schlichting & Levin 1988).

7.5 Literature Cited

Bradshaw, A.D. (1965) Evolutionary significance of phenotypic plasticity in plants. Advances in Genetics 13, 115-155.

Chapin, F.S., III (1991) Effects of multiple environmental stresses on nutrient availability and use. In: Response of Plants to Multiple Stresses (H. A. Mooney, W. E. Winner and E. J. Pell), 67-88. Academic Press, San Diego.

Cordell, S., Goldstein, G., Mueller-Dombois, D., Webb, D. & Vitousek, P.M. (1998) Physiological and morphological variation in *Metrosideros polymorpha*, a dominant Hawaiian tree species, along an altitudinal gradient: the role of phenotypic plasticity. Oecologia 113, 188-196.

Crick, J.C. & Grime, J.P. (1987) Morphological plasticity and mineral nutrients capture in two herbaceous species of contrasting ecology. New Phytologist 107, 403-414.

Ehleringer, J.R. (1993) Carbon and water relations in desert plants: an isotopic perspective. In: Stable Isotopes and plant carbon- water relations (J. R. Ehleringer, A. E. Hall and G. D. Farquhar), 155-172. Academic Press, New York.

Ehleringer, J.R. (1993) Variation in leaf carbon isotope discrimination in *Encelia farinosa* implications for growth, competition, and drought survival. Oecologia 95, 340-346.

Grime, J.P., Crick, J.C. & Rincon, J.E. (1986) The ecological significance of plasticity. In: Plasticity in plants (D. H. Jennings and A. J. Trewavas), 5-29. Company of Biologists, Cambridge.

Hutchings, M.J. & de Kroon, H. (1994) Foraging in plants: the role of morphological plasticity in resource acqusition. Advances in ecological research 25, 159-238.

Lambers, H. & Poorter, H. (1992) Inherent variation in growth rate between higher plants: a search for physiological causes and ecological consequences. Advances in Ecological Research 23, 187-261.

Palmroth, S., Berninger, F., Nikinmass, E., Lloyd, J., Pulkkinen, P. & Hari, P. (1999) Structural adaptation rather than water conservation was observed in Scots pine over a range of wet to dry conditions. Oecologia 121, 302-309.

Scheiner, S.M. (1993) Genetics and evolution of phenotypic plasticity. Annu. Rev. Ecol. Syst. 24, 35-68.

Schlichting, C.D. & Levin, D.A. (1988) Phenotypic plasticity in Phlox. Land and cultivated populations of *P. drummondii*. Amer. J. Bot 75, 161-169.

7.6 Tables and Figures

Table 7.1 Species groups based on overlapping latitudinal distributions.

Species	Latitudinal midpoint of sampled distribution and ranges of non-significant differences		
E. miniata	13.8300	A	
		A	
E. tetrodonta	13.9417	A	
		A	
E. tectifica	14.0046	A	
E. confertiflora	15.1488	B	
		B	
E. chlorophylla	15.3463	B	
E. dichromophloia	16.2331	C	
E. coolabah	17.2924	D	
		D	
E. pruinosa	17.6275	D	E
			E
E. leucophloia	18.1984		E
E. odontocarpa	19.6091	F	
		F	
E. terminalis	20.2111	F	G
			G
E. pachyphylla	20.7703		G
E. gamophylla	23.4935	H	

Figure Legends

Figure 7.1

Species mean (± SE) measured values in relation to the location of the midpoint of the distribution of the species along the transect. In this, and subsequent Figures, where there was a significant trend (α=0.05) the regression lines are shown.

Figure 7.2

Species mean (± SE) calculated values in relation to the location of the midpoint of the distribution of the species along the transect.

Figure 7.3

The change in the measured values of each species, determined from the endpoints of the linear regressions, in relation to the location of the species along the transect or the size of the distributional range of the species along the transect.

Figure 7.4

The change in the calculated values of each species, determined from the endpoint of the linear regressions, in relation to the location of the species along the transect or the size of the distributional range of the species along the transect.

Figure 7.5

The elasticities of the linear relationships between the measured values and latitude in relation to the location and the size of the distribution of the species along the transect.

Figure 7.6

The elasticities of the linear relationships between the calculated values and latitude in relation to the location and the size of the distribution of the species along the transect.

Figure 7.7

The elasticities of the measured values in response to the changes in rainfall within the distribution of each species.

Figure 7.8

The elasticities of the calculated values in response to the changes in rainfall within the distribution of each species.

Figure 7.9

The coefficient of variation of the measured and calculated values across the distribution of *E. miniata.*

Figure 7.10

The coefficient of variation of the measured and calculated values across the distribution of *E. tetrodonta.*

Figure 7.11

The coefficient of variation of the measured and calculated values across the distribution of *E. tectifica.*

Figure 7.12

The coefficient of variation of the measured and calculated values across the distribution of *E. confertiflora.*

Figure 7.13

The coefficient of variation of the measured and calculated values across the distribution of *E. dichromophloia.*

Figure 7.14

The coefficient of variation of the measured and calculated values across the distribution of *E. chlorophylla.*

Figure 7.15

The coefficient of variation of the measured and calculated values across the distribution of *E. pruinosa.*

Figure 7.16

The coefficient of variation of the measured and calculated values across the distribution of *E. coolabah.*

Figure 7.17

The coefficient of variation of the measured and calculated values across the distribution of *E. leucophloia.*

Figure 7.18

The coefficient of variation of the measured and calculated values across the distribution of *E. terminalis.*

Figure 7.19

The coefficient of variation of the measured and calculated values across the distribution of *E. odontocarpa.*

Figure 7.20

The coefficient of variation of the measured and calculated values across the distribution of *E. pachyphylla.*

Figure 7.21

The coefficient of variation of the measured and calculated values across the distribution of *E. gamophylla.*

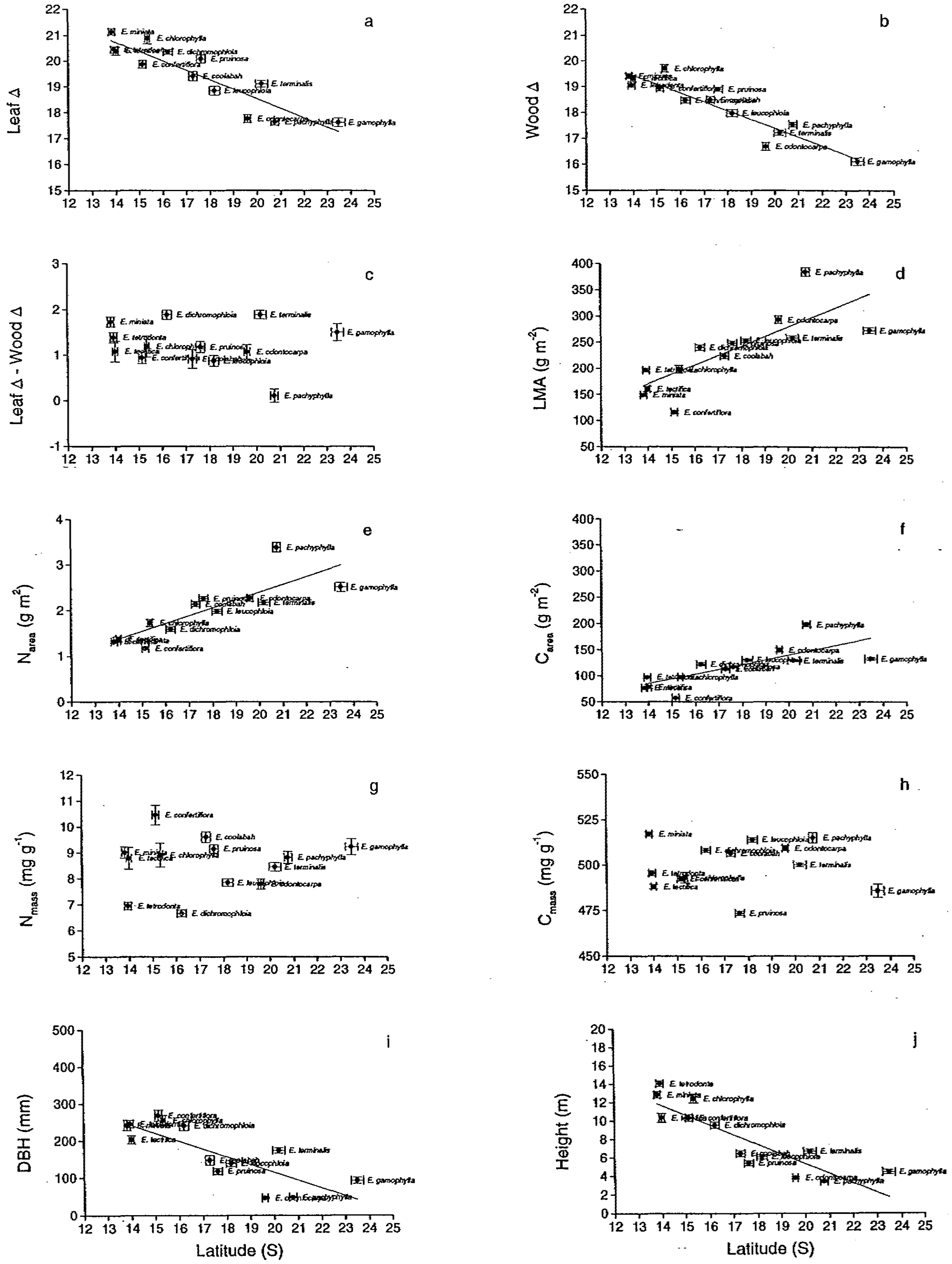

a
Leaf Δ
b
Wood Δ
c
Leaf Δ - Wood Δ
d
LMA (g m^{-2})
e
N_{area} (g m^{2})
f
C_{area} (g m^{-2})
g
N_{mass} (mg g^{-1})
h
C_{mass} (mg g^{-1})
i
DBH (mm)
j
Height (m)
Latitude (S)
Latitude (S)
E. miniata
E. chlorophylla
E. tetrodonta
E. dichromophloia
E. pruinosa
E. confertiflora
E. coolabah
E. terminalis
E. leucophloia
E. odontocarpa
E. pachyphylla
E. gamophylla
E. tectifica

Figure 7.1

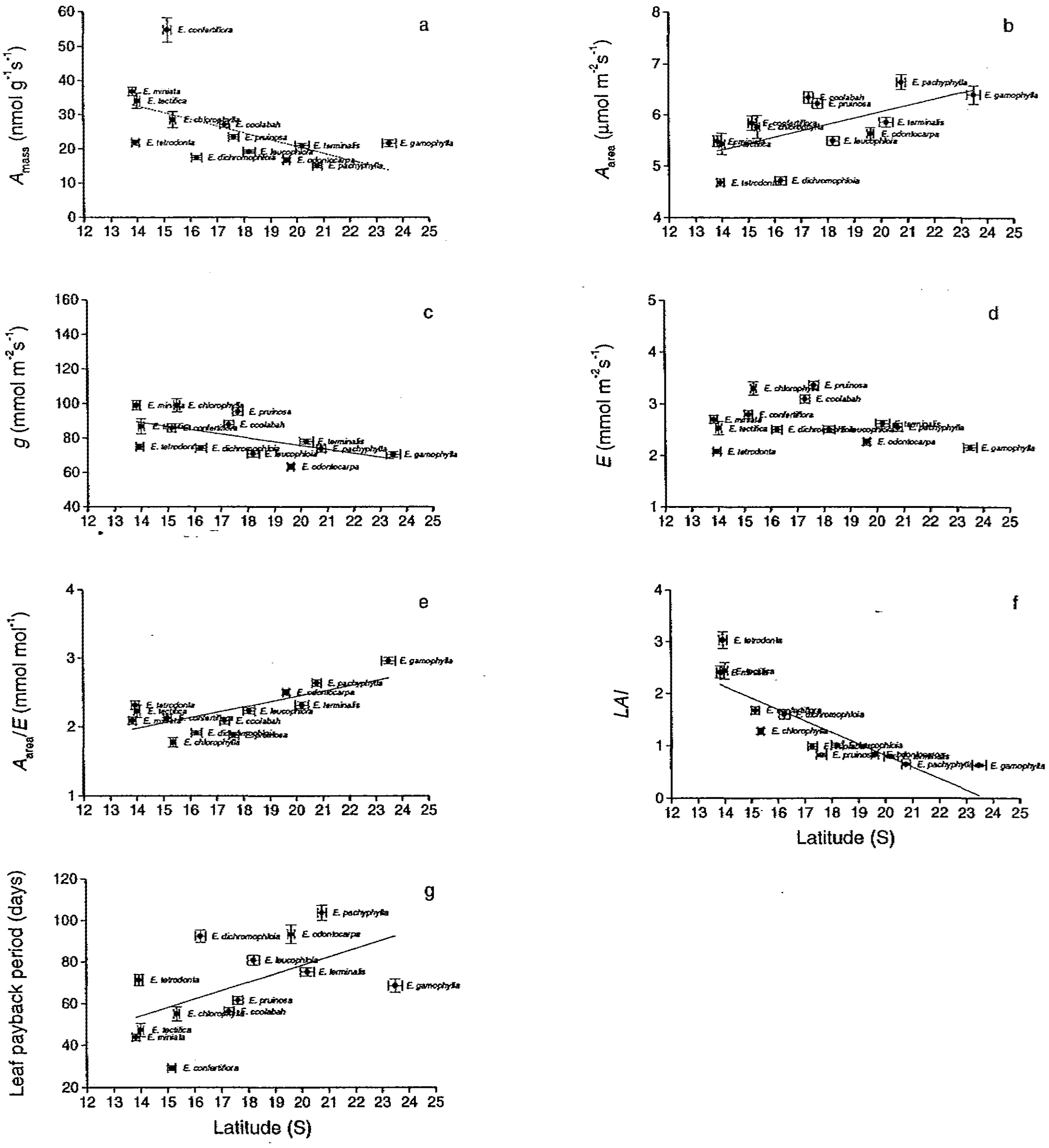

a
A_{mass} (nmol g^{-1}s^{-1})
b
A_{area} (µmol m^{-2}s^{-1})
c
g (mmol m^{-2}s^{-1})
d
E (mmol m^{-2}s^{-1})
e
A_{area}/E (mmol mol^{-1})
f
LAI
g
Leaf payback period (days)
Latitude (S)
12 13 14 15 16 17 18 19 20 21 22 23 24 25
E. confertiflora
E. miniata
E. tectifica
E. chlorophylla
E. coolabah
E. pruinosa
E. tetrodonta
E. dichromophloia
E. leucophloia
E. terminalis
E. odontocarpa
E. pachyphylla
E. gamophylla

Figure 7.2

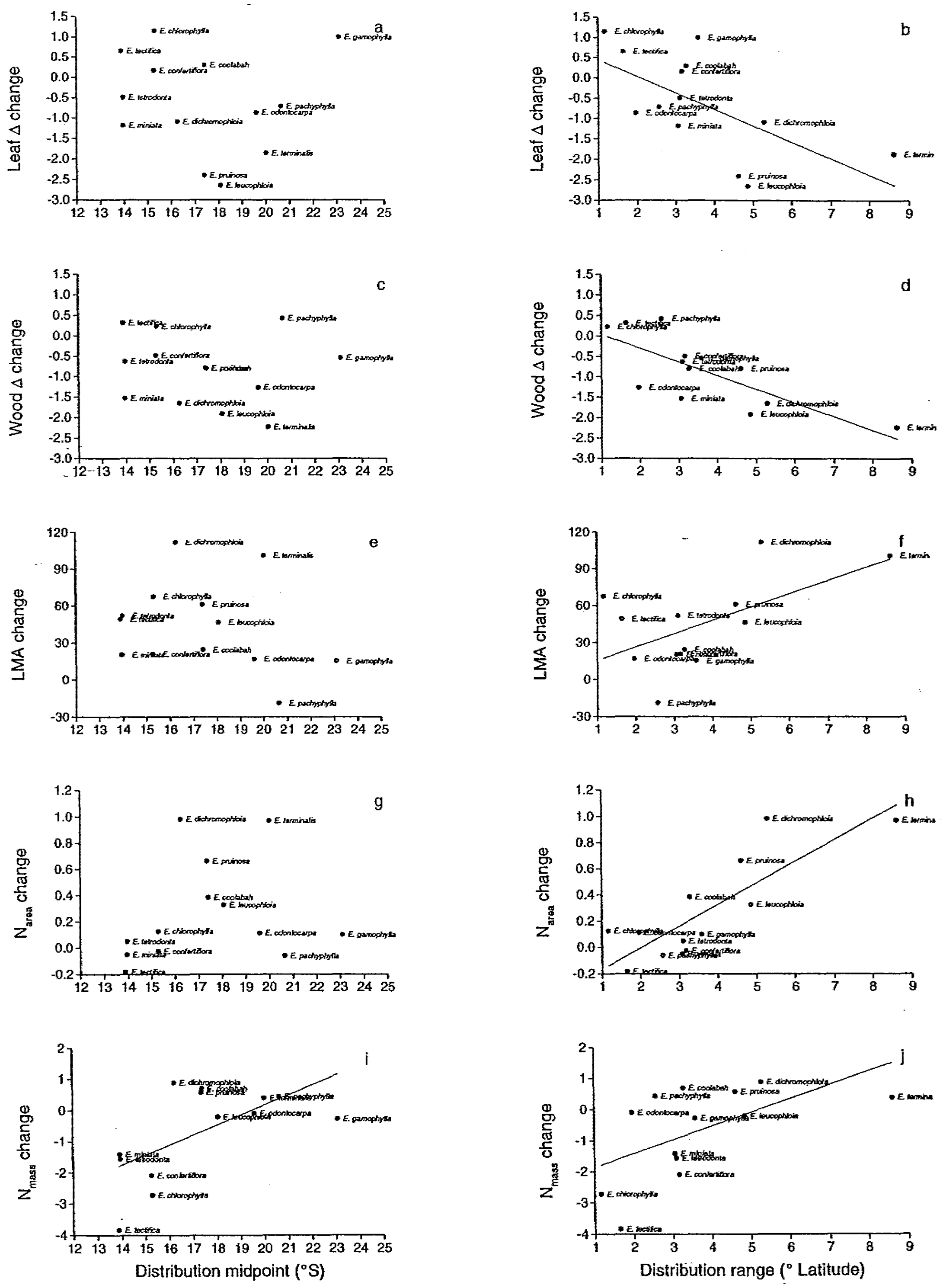

a
b
c
d
e
f
g
h
i
j
Leaf Δ change
Wood Δ change
LMA change
N_{area} change
N_{mass} change
1.5
1.0
0.5
0.0
-0.5
-1.0
-1.5
-2.0
-2.5
-3.0
120
90
60
30
0
-30
1.2
0.8
0.6
0.4
0.2
-0.2
2
1
0
-1
-2
-3
-4
12 13 14 15 16 17 18 19 20 21 22 23 24 25
1 2 3 4 5 6 7 8 9
E. chlorophylla
E. gamophylla
E. tectifica
E. confertiflora
E. coolabah
E. tetrodonta
E. pachyphylla
E. odontocarpa
E. miniata
E. dichromophloia
E. terminalis
E. pruinosa
E. leucophloia
Distribution midpoint (°S)
Distribution range (° Latitude)

Figure 7.3

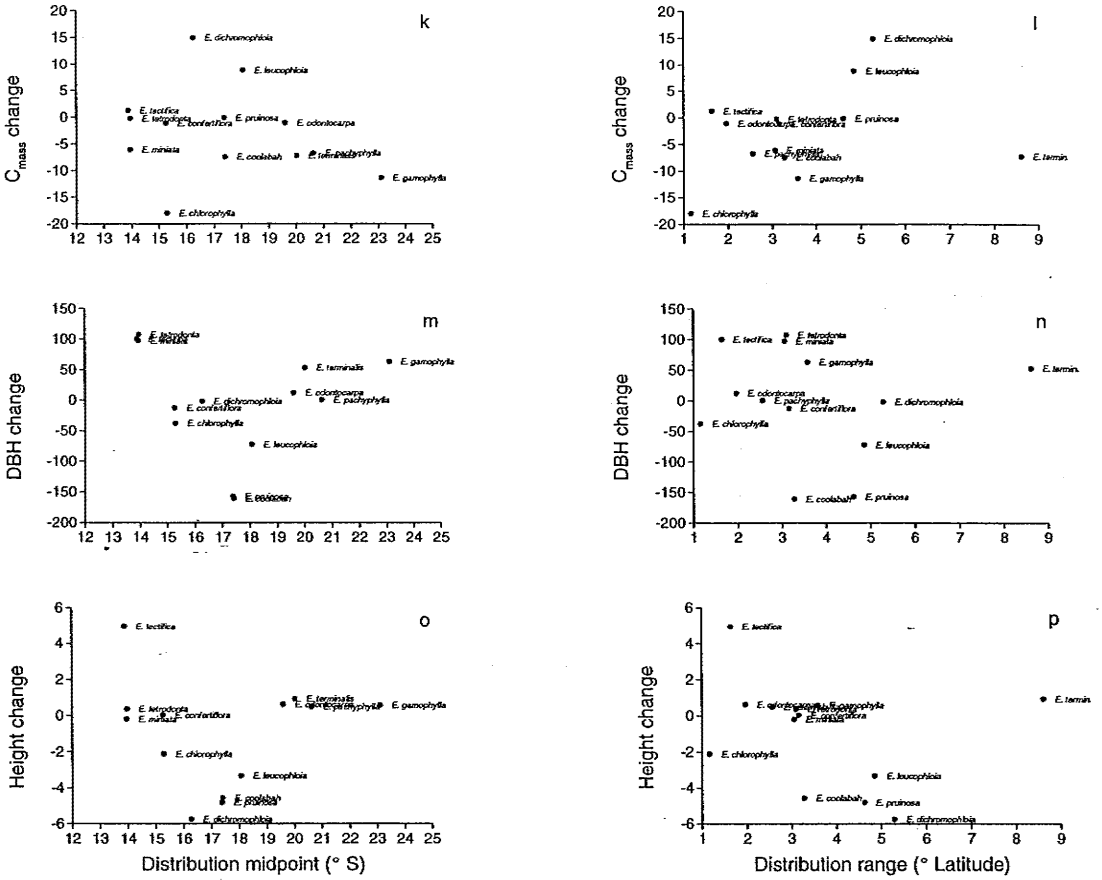


Figure 7.3 (continued)

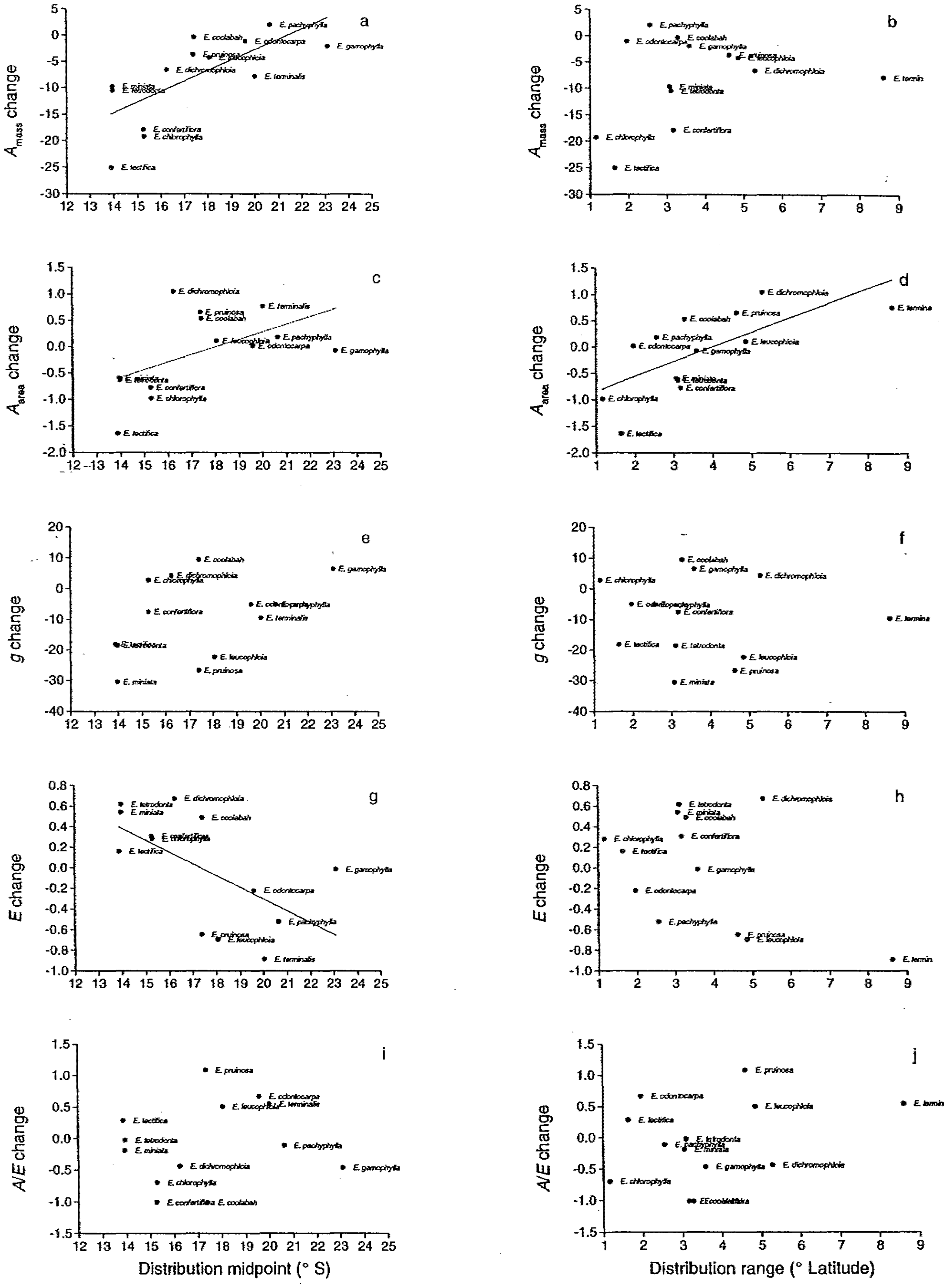
a
b
c
d
e
f
g
h
i
j
A_{mass} change
A_{area} change
g change
E change
A/E change
5
0
-5
-10
-15
-20
-25
-30
1.5
1.0
0.5
0.0
-0.5
-1.0
-1.5
-2.0
20
10
-40
0.8
0.6
0.4
0.2
-0.2
-0.4
-0.6
-0.8
12 13 14 15 16 17 18 19 20 21 22 23 24 25
1 2 3 4 5 6 7 8 9
E. pachyphylla
E. coolabah
E. odontocarpa
E. gamophylla
E. pruinosa
E. leucophloia
E. dichromophloia
E. terminalis
E. miniata
E. tetrodonta
E. confertiflora
E. chlorophylla
E. tectifica
E. termin
E. termina
Distribution midpoint (° S)
Distribution range (° Latitude)

Figure 7.4

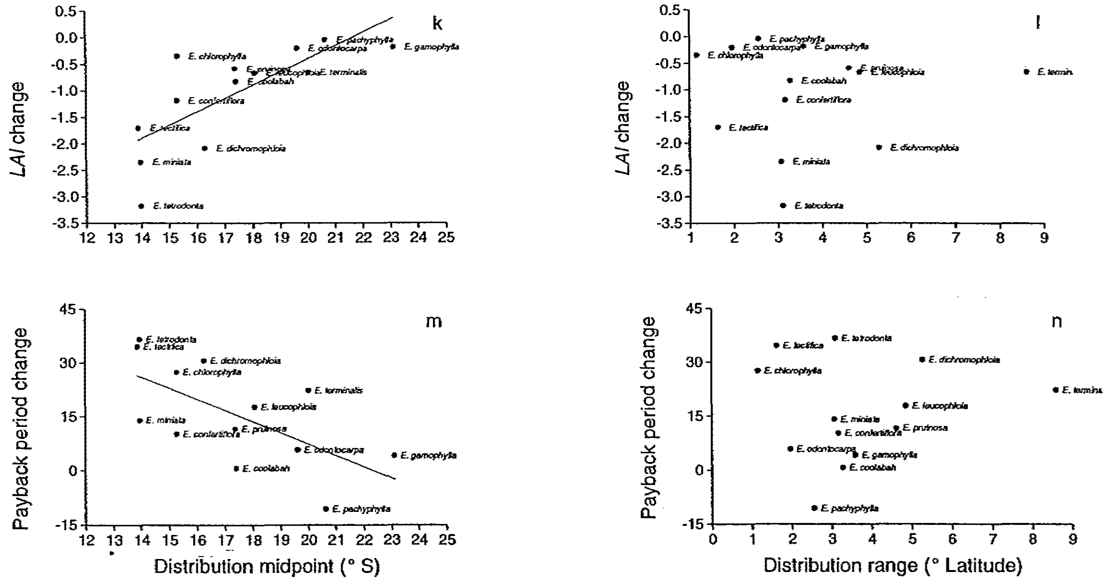


Figure 7.4 (continued)

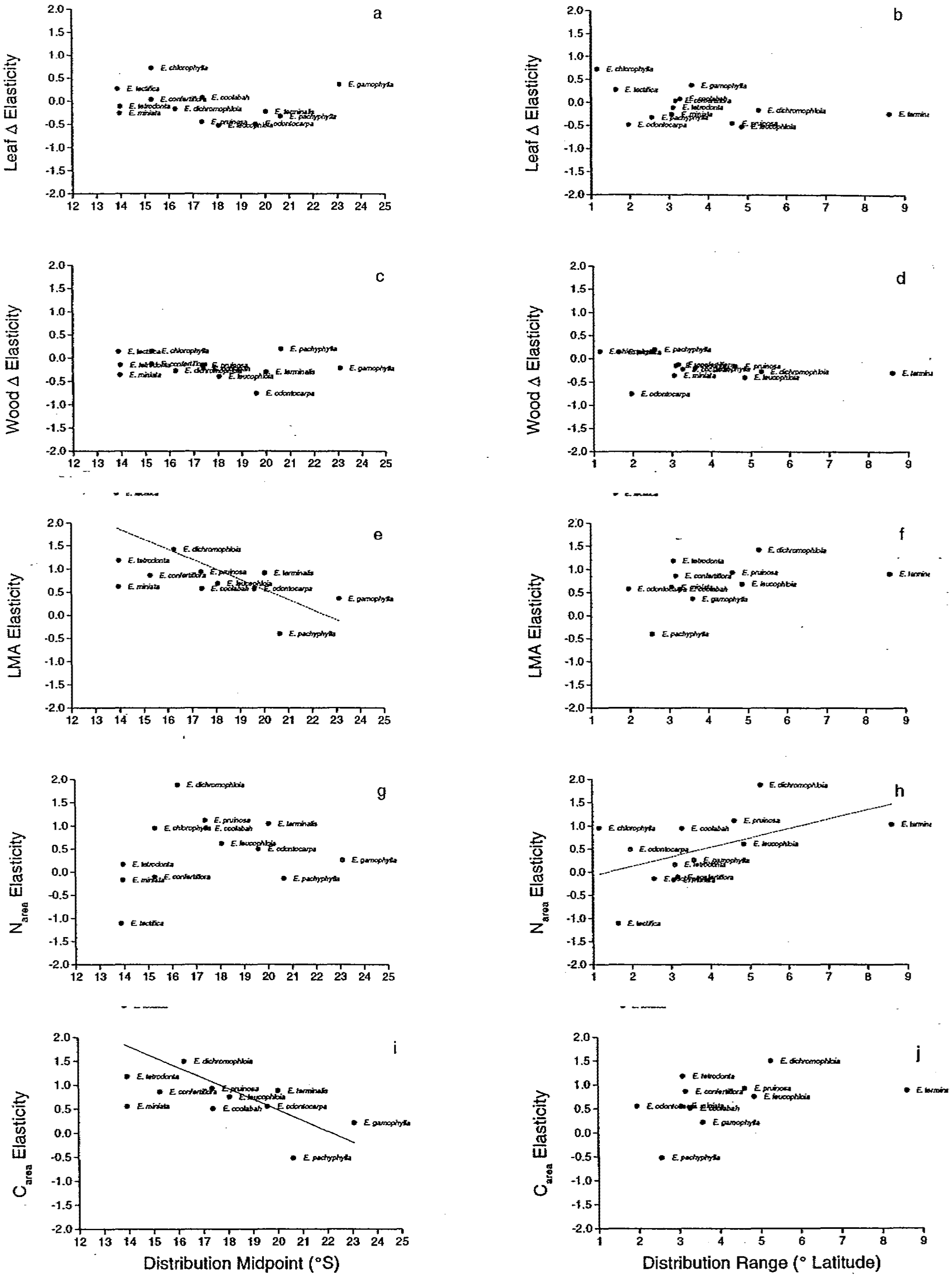

a
b
c
d
e
f
g
h
i
j
Leaf Δ Elasticity
Wood Δ Elasticity
LMA Elasticity
N_{area} Elasticity
C_{area} Elasticity
2.0
1.5
1.0
0.5
0.0
-0.5
-1.0
-1.5
-2.0
12
13
14
15
16
17
18
19
20
21
22
23
24
25
1
2
3
4
5
6
7
8
9
E. chlorophylla
E. tectifica
E. gamophylla
E. confertiflora
E. coolabah
E. tetrodonta
E. miniata
E. dichromophloia
E. terminalis
E. pachyphylla
E. pruinosa
E. leucophloia
E. odontocarpa
Distribution Midpoint (°S)
Distribution Range (° Latitude)

Figure 7.5

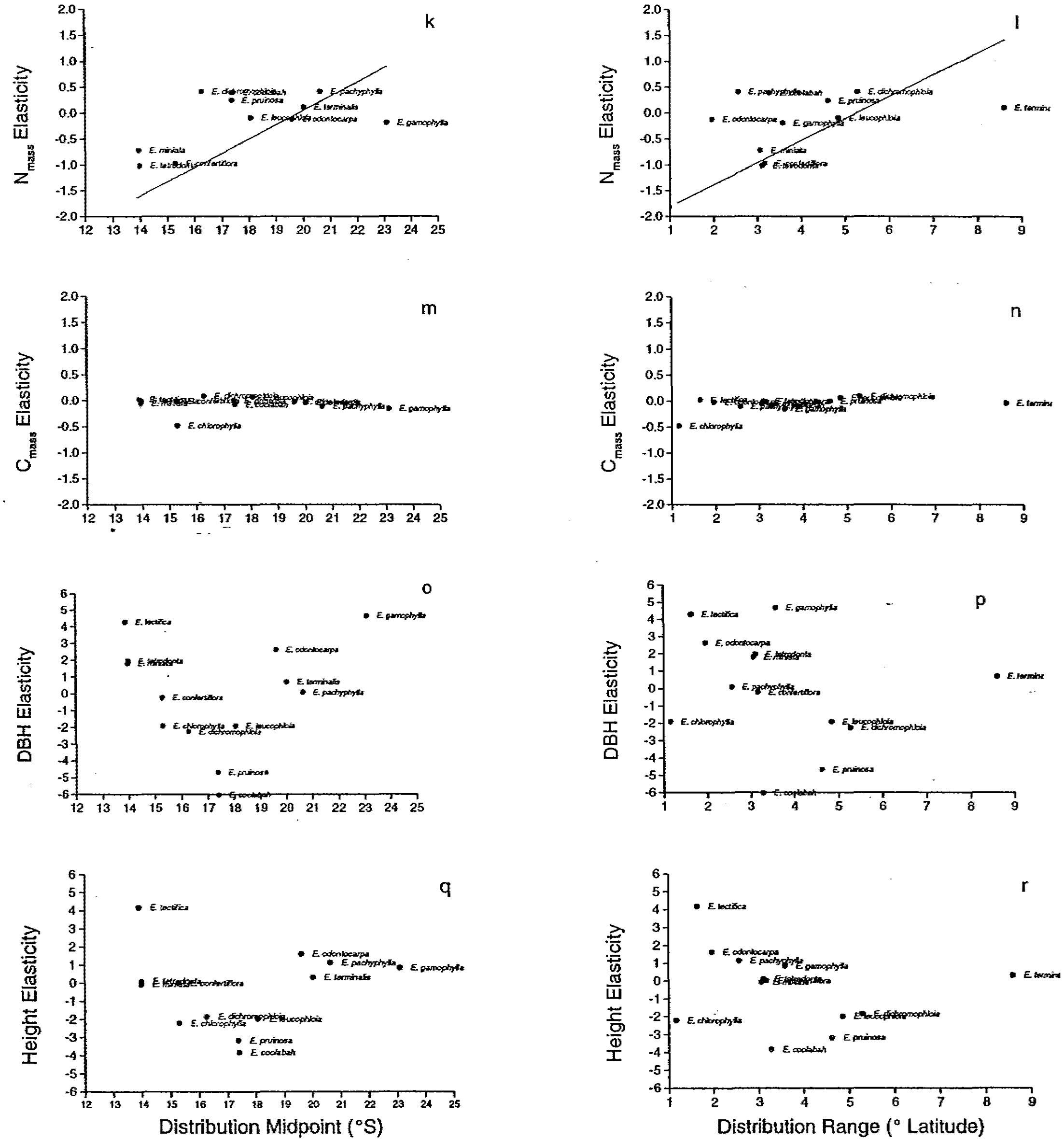


Figure 7.5 (continued)

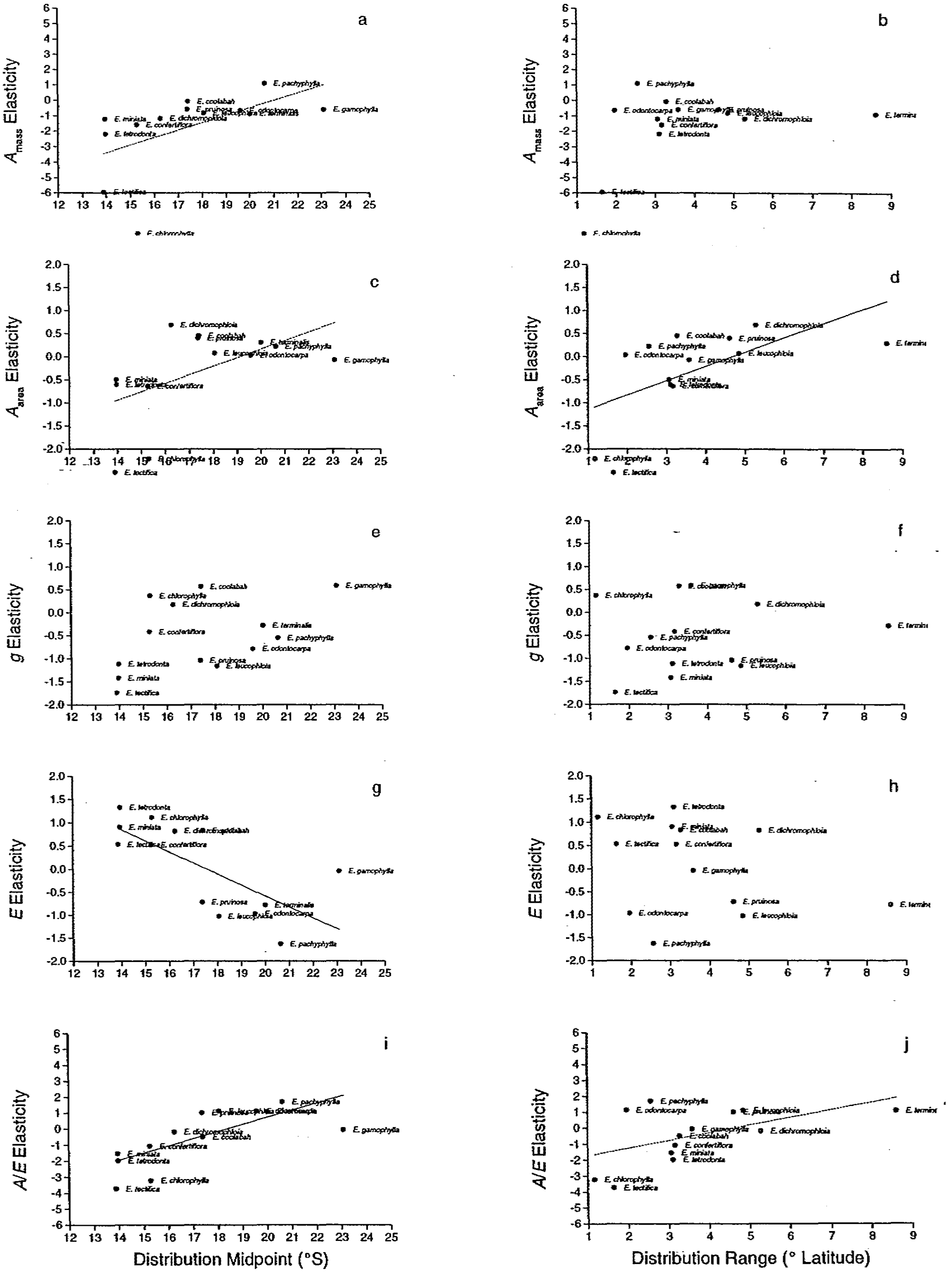

a
b
c
d
e
f
g
h
i
j
A_{mass} Elasticity
A_{area} Elasticity
g Elasticity
E Elasticity
A/E Elasticity
6
5
4
3
2
1
0
-1
-2
-3
-4
-5
-6
2.0
1.5
1.0
0.5
0.0
-0.5
-1.0
-1.5
-2.0
12
13
14
15
16
17
18
19
20
21
22
23
24
25
1
2
3
4
5
6
7
8
9
E. pachyphylla
E. coolabah
E. pruinosa
E. odontocarpa
E. leucophloia
E. terminalis
E. gamophylla
E. miniata
E. dichromophloia
E. confertiflora
E. tetrodonta
E. tectifica
E. chlorophylla
Distribution Midpoint (°S)
Distribution Range (° Latitude)

Figure 7.6

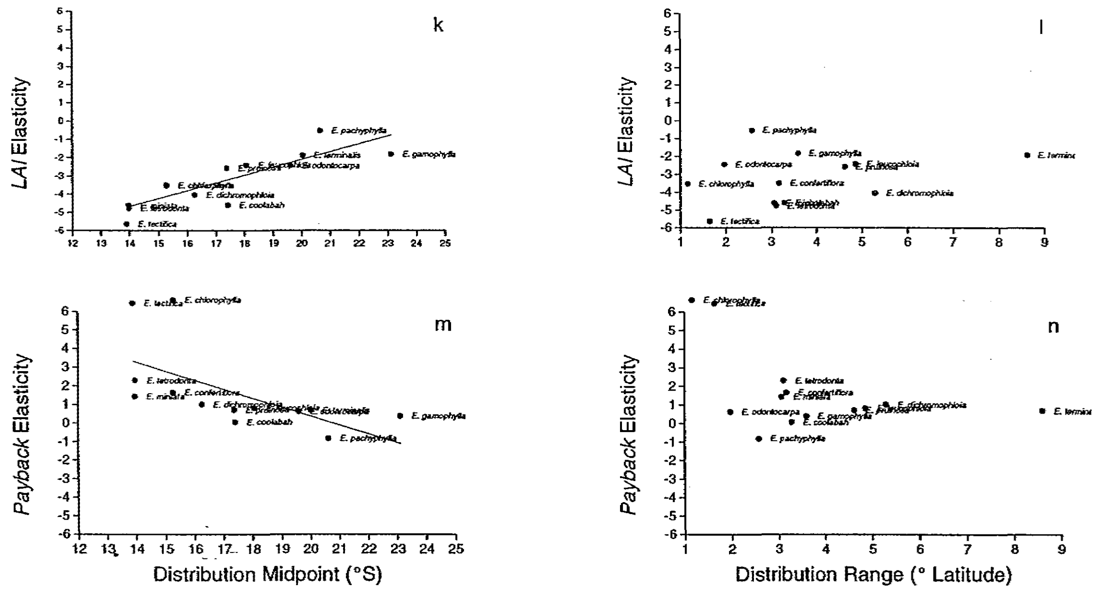


Figure 7.6 (continued)

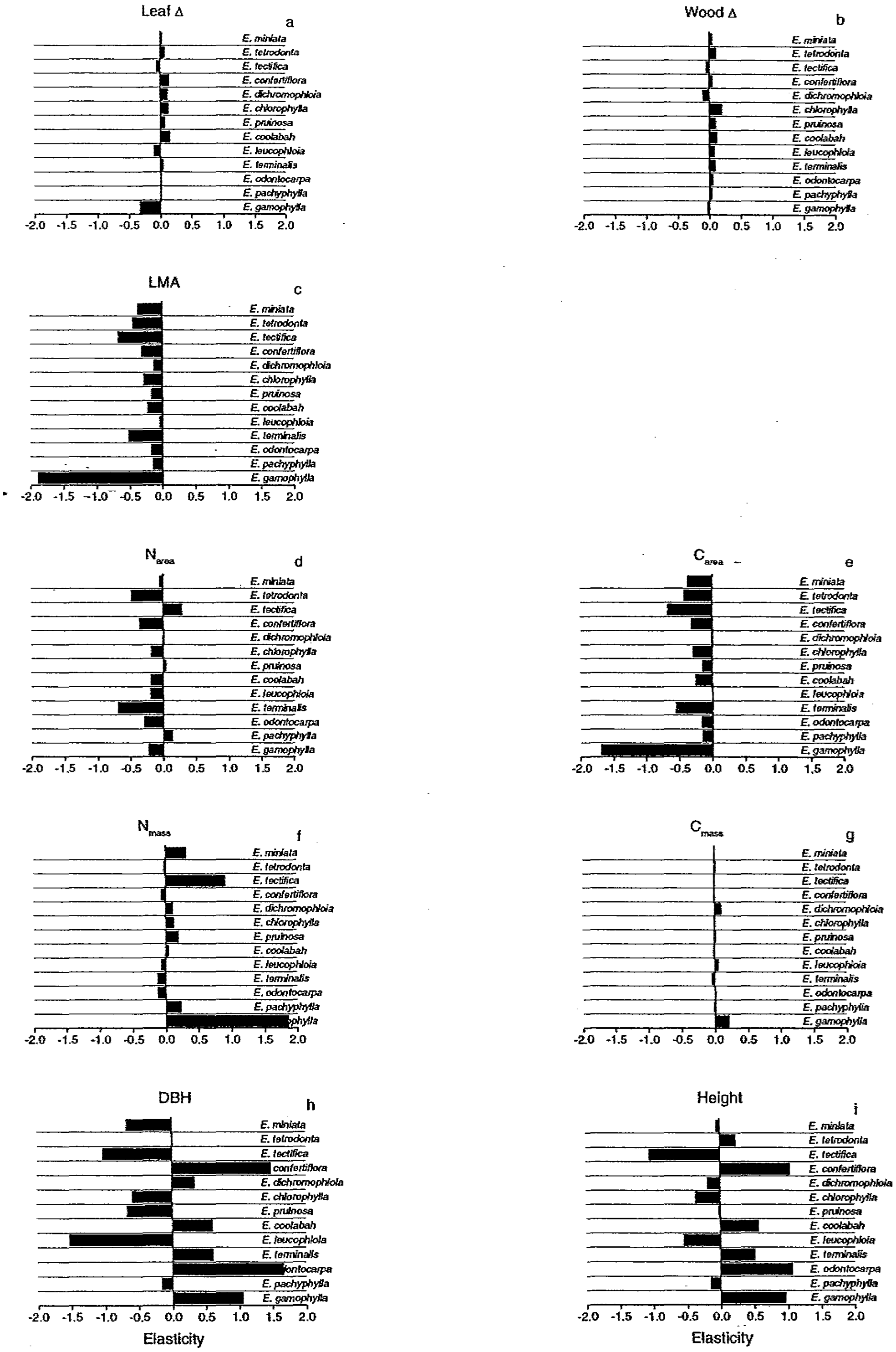

Leaf Δ
a
Wood Δ
b
LMA
c
N$_{area}$
d
C$_{area}$
e
N$_{mass}$
f
C$_{mass}$
g
DBH
h
Height
i
E. miniata
E. tetrodonta
E. tectifica
E. confertiflora
E. dichromophloia
E. chlorophylla
E. pruinosa
E. coolabah
E. leucophloia
E. terminalis
E. odontocarpa
E. pachyphylla
E. gamophylla
-2.0
-1.5
-1.0
-0.5
0.0
0.5
1.0
1.5
2.0
Elasticity

Figure 7.7

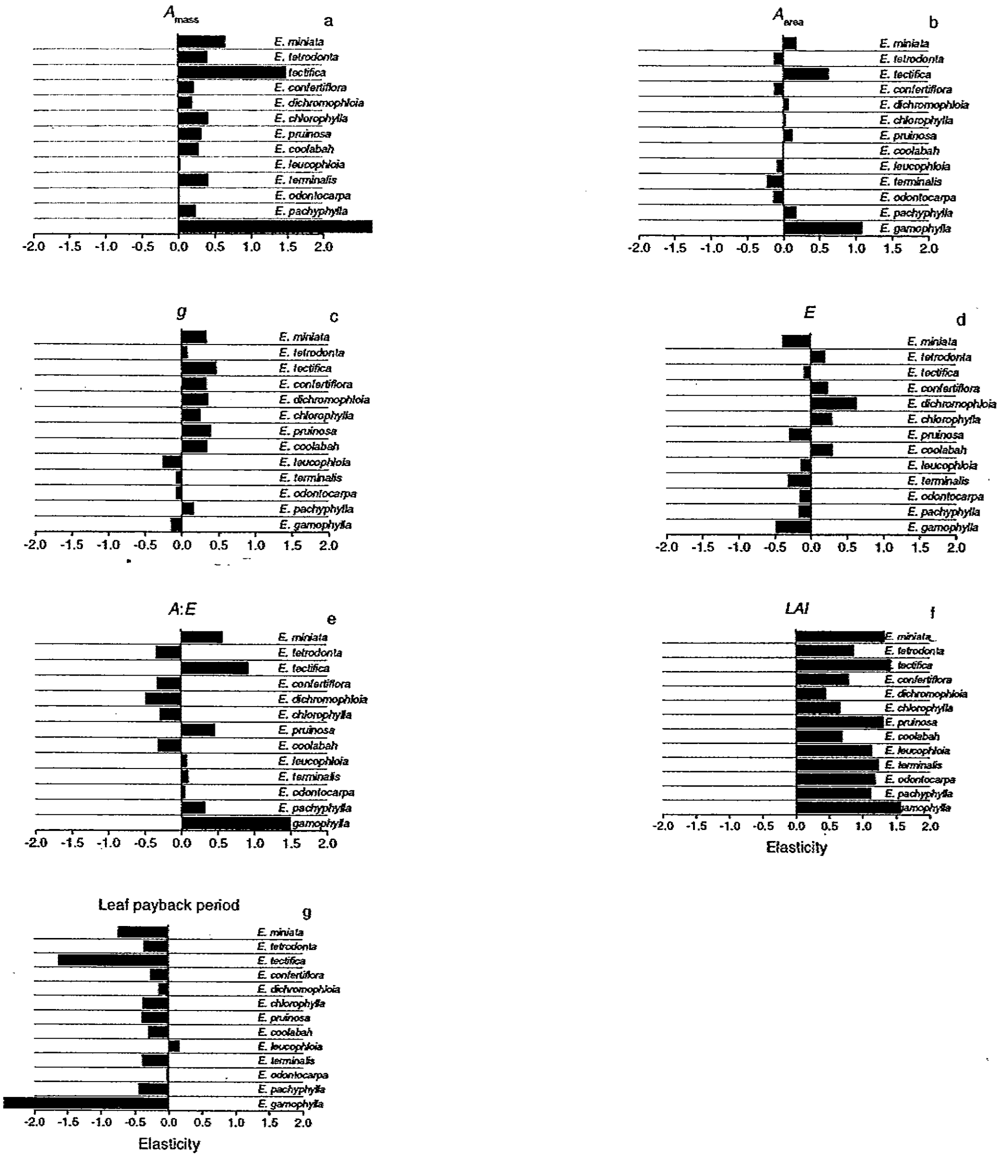

A_{mass}
a
E. miniata
E. tetrodonta
tectifica
E. confertiflora
E. dichromophloia
E. chlorophylla
E. pruinosa
E. coolabah
E. leucophloia
E. terminalis
E. odontocarpa
E. pachyphylla
-2.0 -1.5 -1.0 -0.5 0.0 0.5 1.0 1.5 2.0
A_{area}
b
E. miniata
E. tetrodonta
E. tectifica
E. confertiflora
E. dichromophloia
E. chlorophylla
E. pruinosa
E. coolabah
E. leucophloia
E. terminalis
E. odontocarpa
E. pachyphylla
E. gamophylla
-2.0 -1.5 -1.0 -0.5 0.0 0.5 1.0 1.5 2.0
g
c
E. miniata
E. tetrodonta
E. tectifica
E. confertiflora
E. dichromophloia
E. chlorophylla
E. pruinosa
E. coolabah
E. leucophloia
E. terminalis
E. odontocarpa
E. pachyphylla
E. gamophylla
-2.0 -1.5 -1.0 -0.5 0.0 0.5 1.0 1.5 2.0
E
d
E. miniata
E. tetrodonta
E. tectifica
E. confertiflora
E. dichromophloia
E. chlorophylla
E. pruinosa
E. coolabah
E. leucophloia
E. terminalis
E. odontocarpa
E. pachyphylla
E. gamophylla
-2.0 -1.5 -1.0 -0.5 0.0 0.5 1.0 1.5 2.0
A:E
e
E. miniata
E. tetrodonta
E. tectifica
E. confertiflora
E. dichromophloia
E. chlorophylla
E. pruinosa
E. coolabah
E. leucophloia
E. terminalis
E. odontocarpa
E. pachyphylla
gamophylla
-2.0 -1.5 -1.0 -0.5 0.0 0.5 1.0 1.5 2.0
LAI
f
E. miniata
E. tetrodonta
tectifica
E. confertiflora
E. dichromophloia
E. chlorophylla
E. pruinosa
E. coolabah
E. leucophloia
E. terminalis
E. odontocarpa
E. pachyphylla
gamophylla
-2.0 -1.5 -1.0 -0.5 0.0 0.5 1.0 1.5 2.0
Elasticity
Leaf payback period
g
E. miniata
E. tetrodonta
E. tectifica
E. confertiflora
E. dichromophloia
E. chlorophylla
E. pruinosa
E. coolabah
E. leucophloia
E. terminalis
E. odontocarpa
E. pachyphylla
E. gamophylla
-2.0 -1.5 -1.0 -0.5 0.0 0.5 1.0 1.5 2.0
Elasticity

Figure 7.8

E. miniata

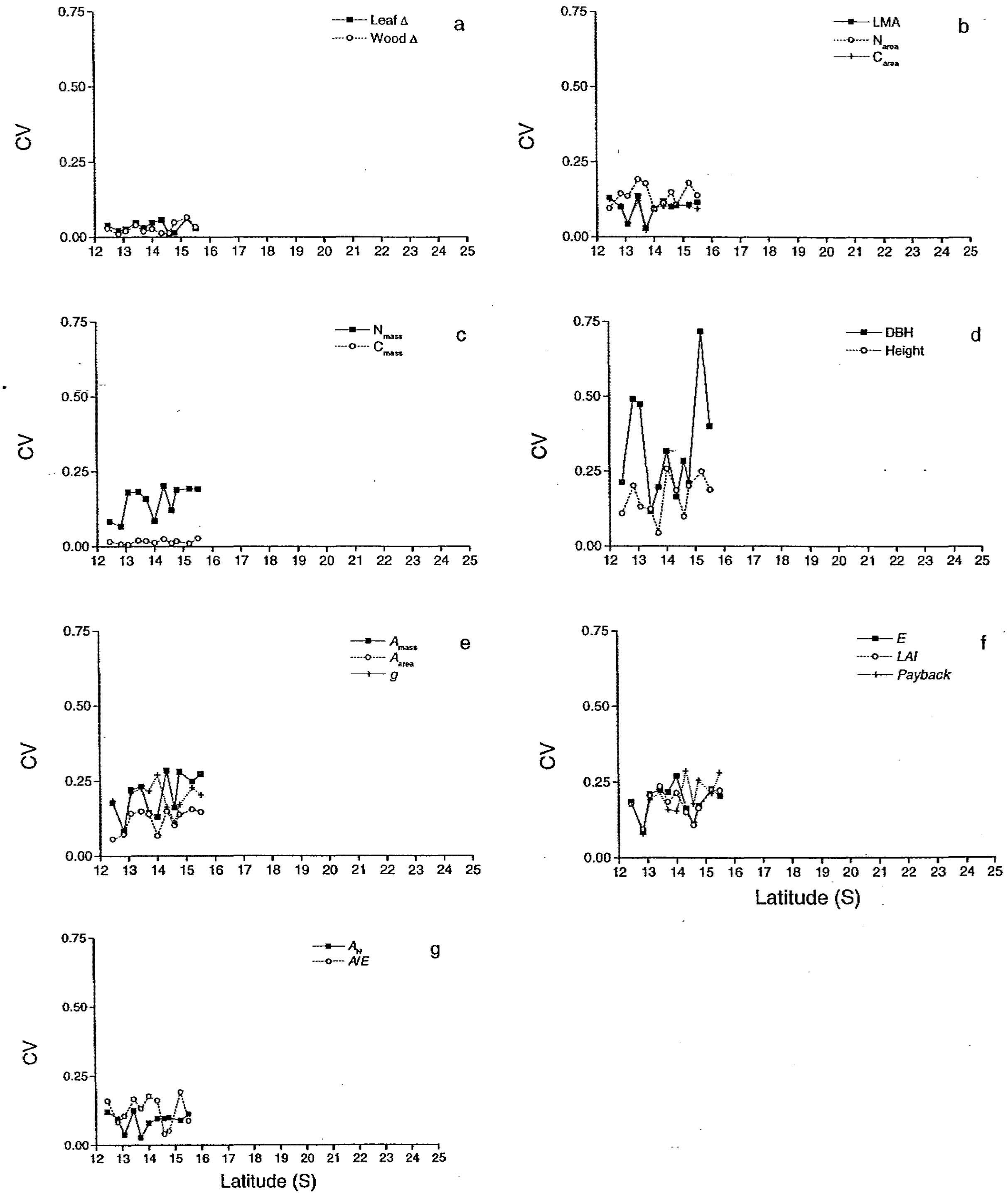


Figure 7.9

E. tetrodonta

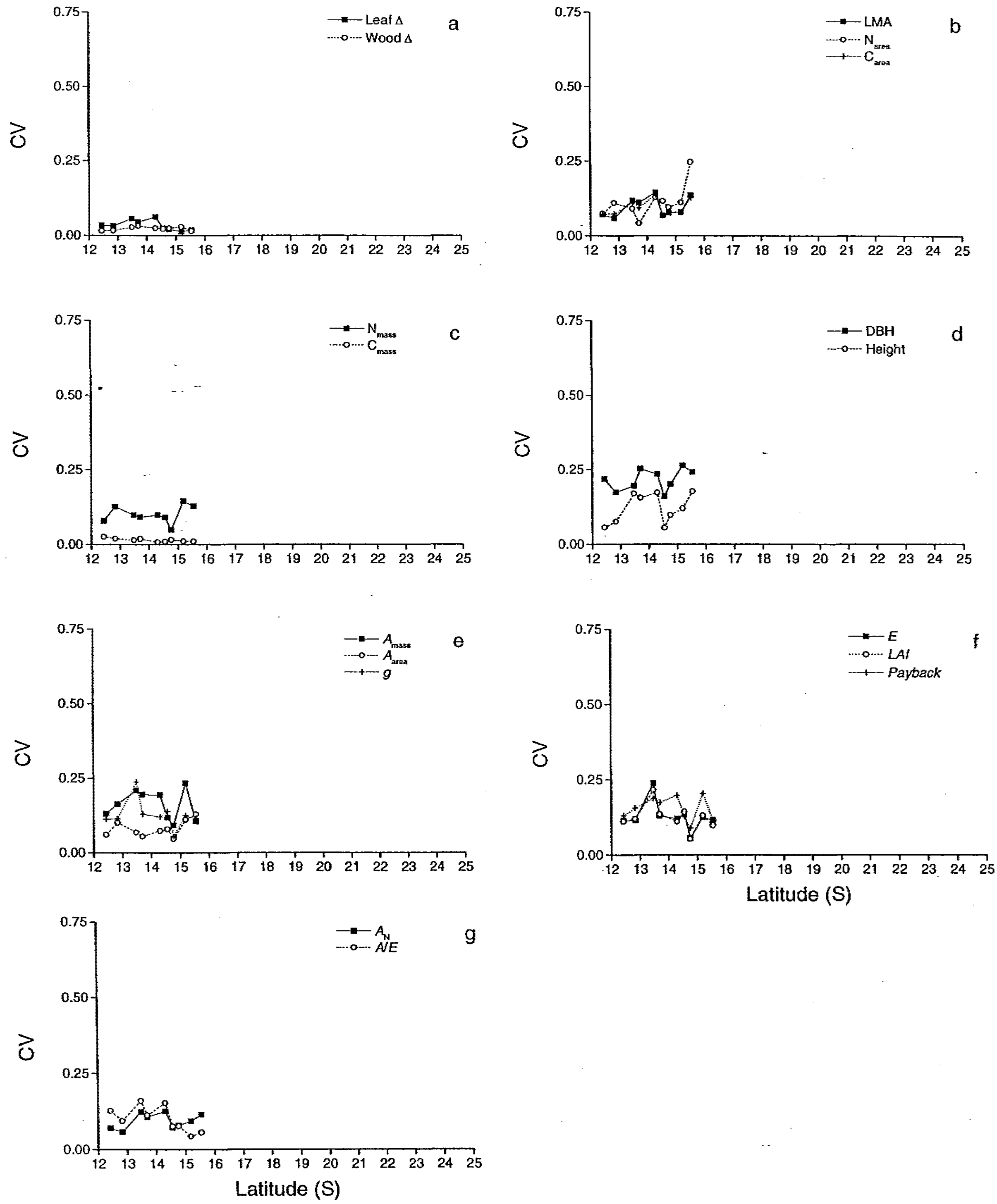


Figure 7.10

E. tectifica

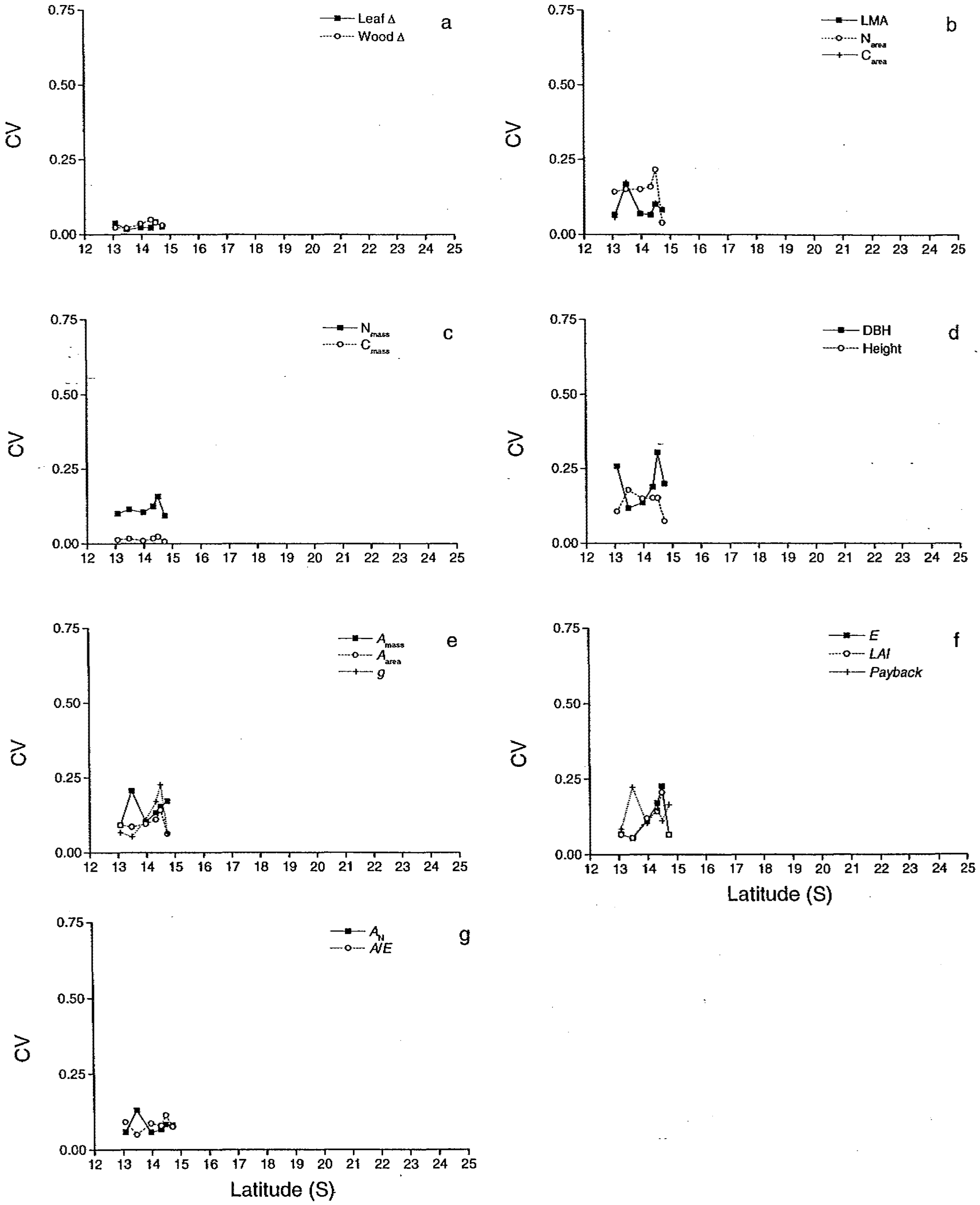


Figure 7.11

E. confertiflora

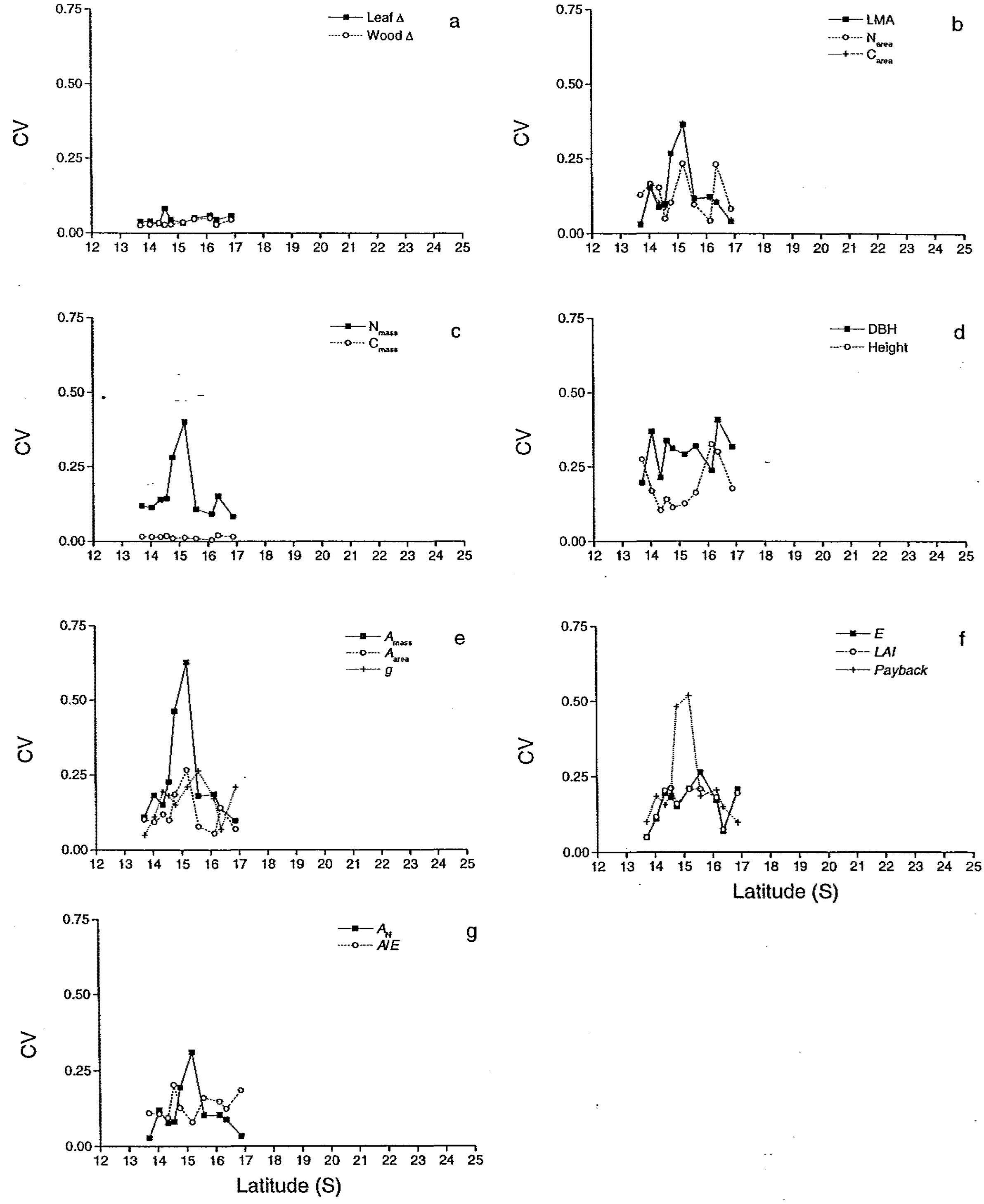


Figure 7.12

E. dichromophloia

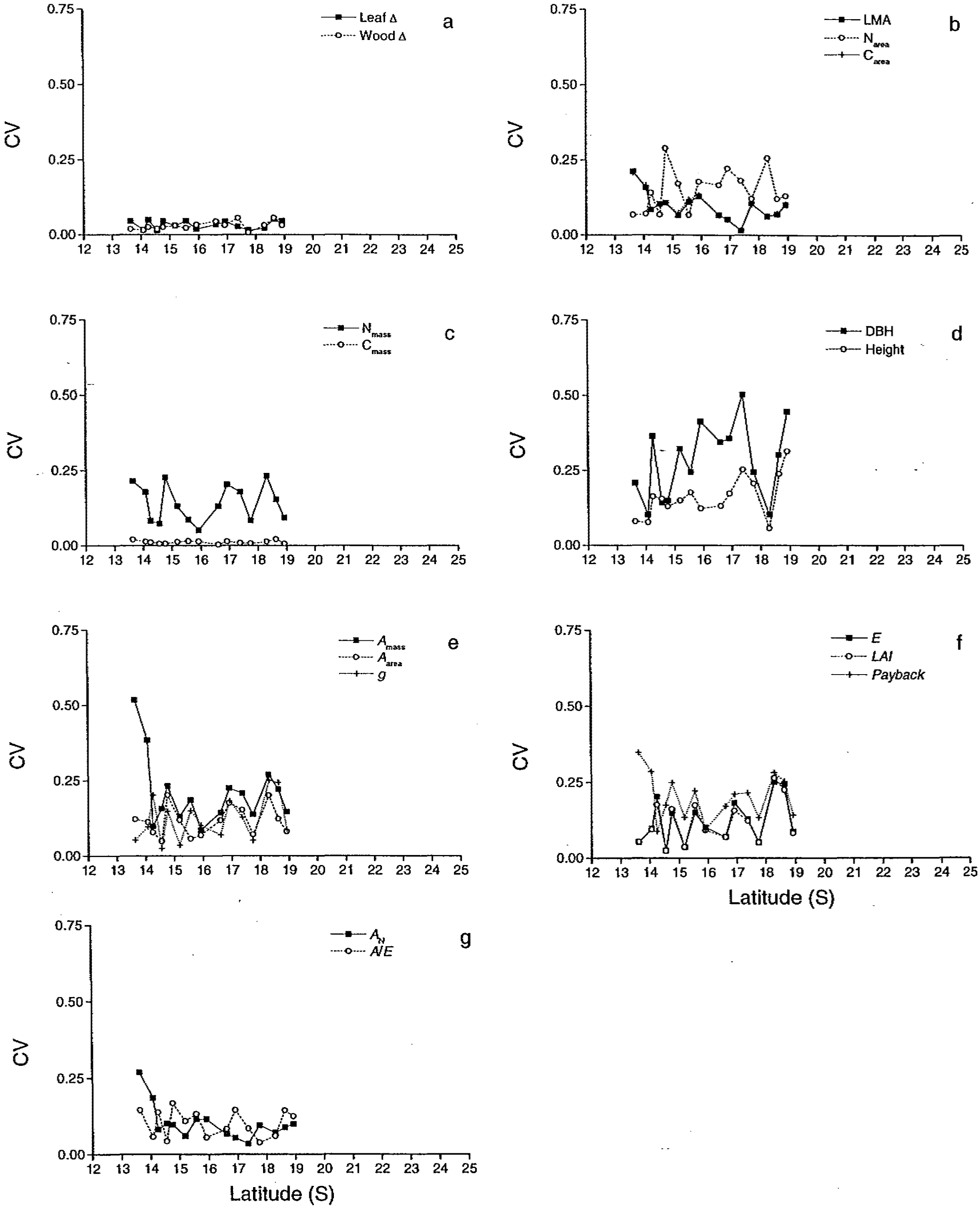


Figure 7.13

E. chlorophylla

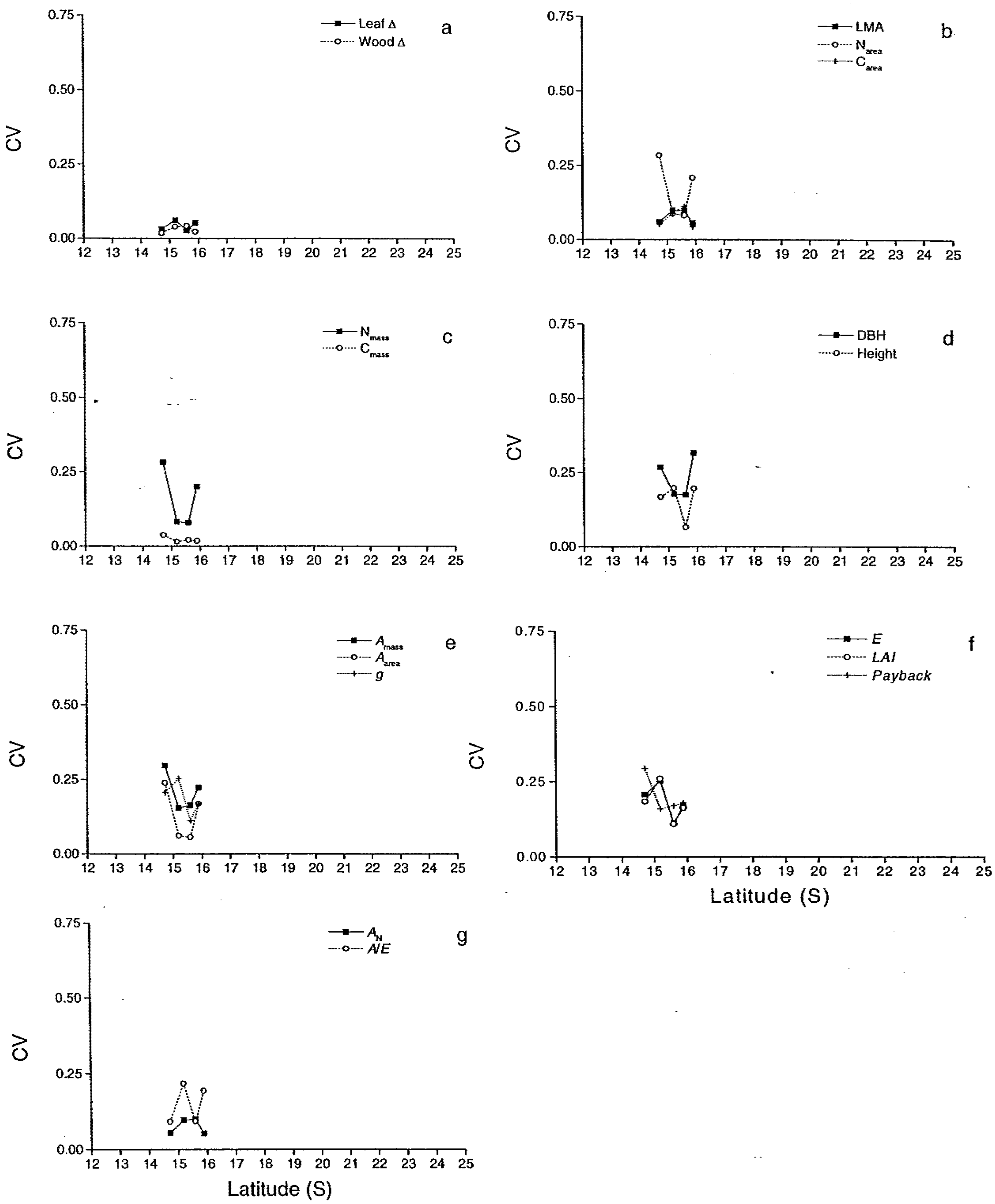


Figure 7.14

E. pruinosa

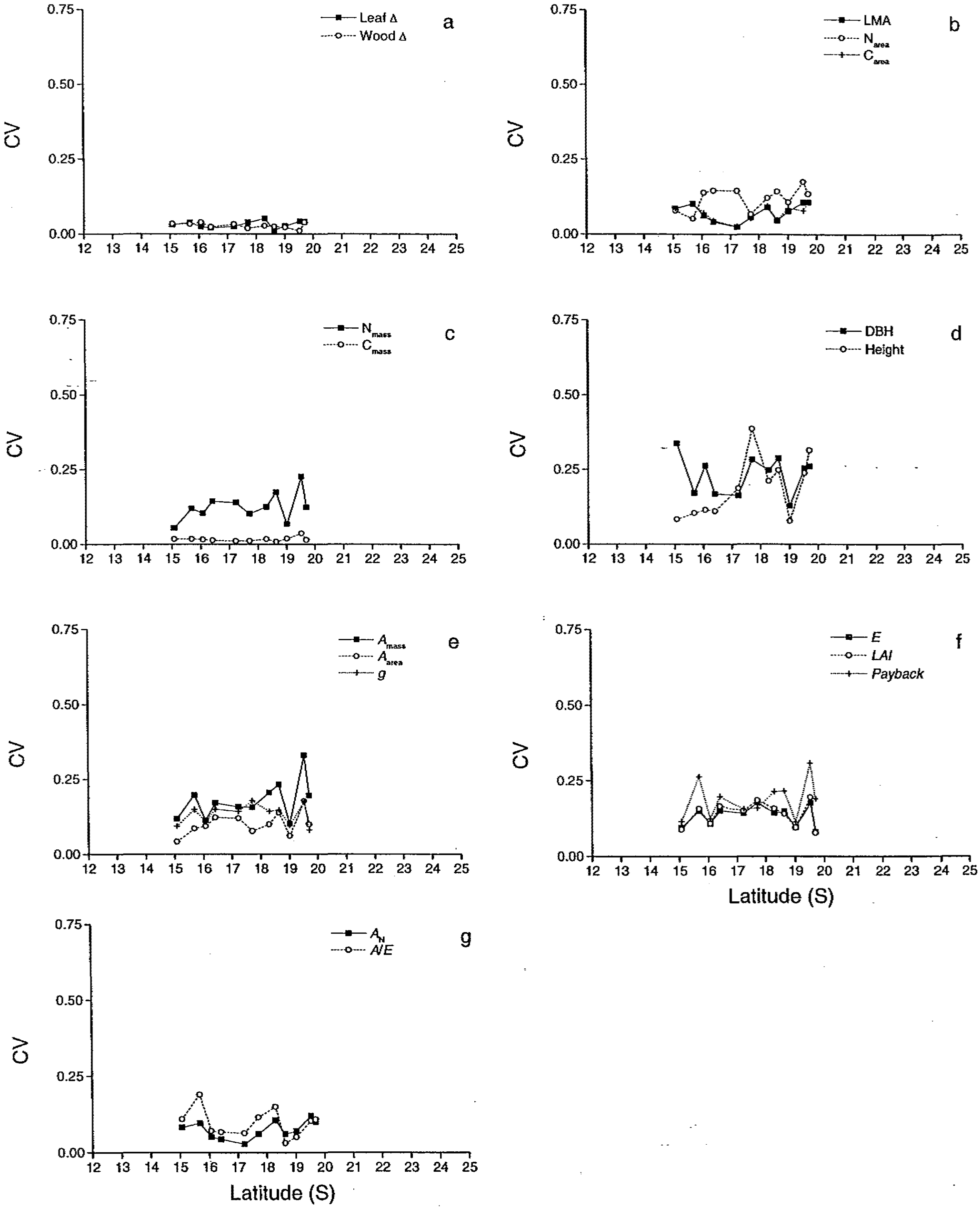


Figure 7.15

E. coolabah

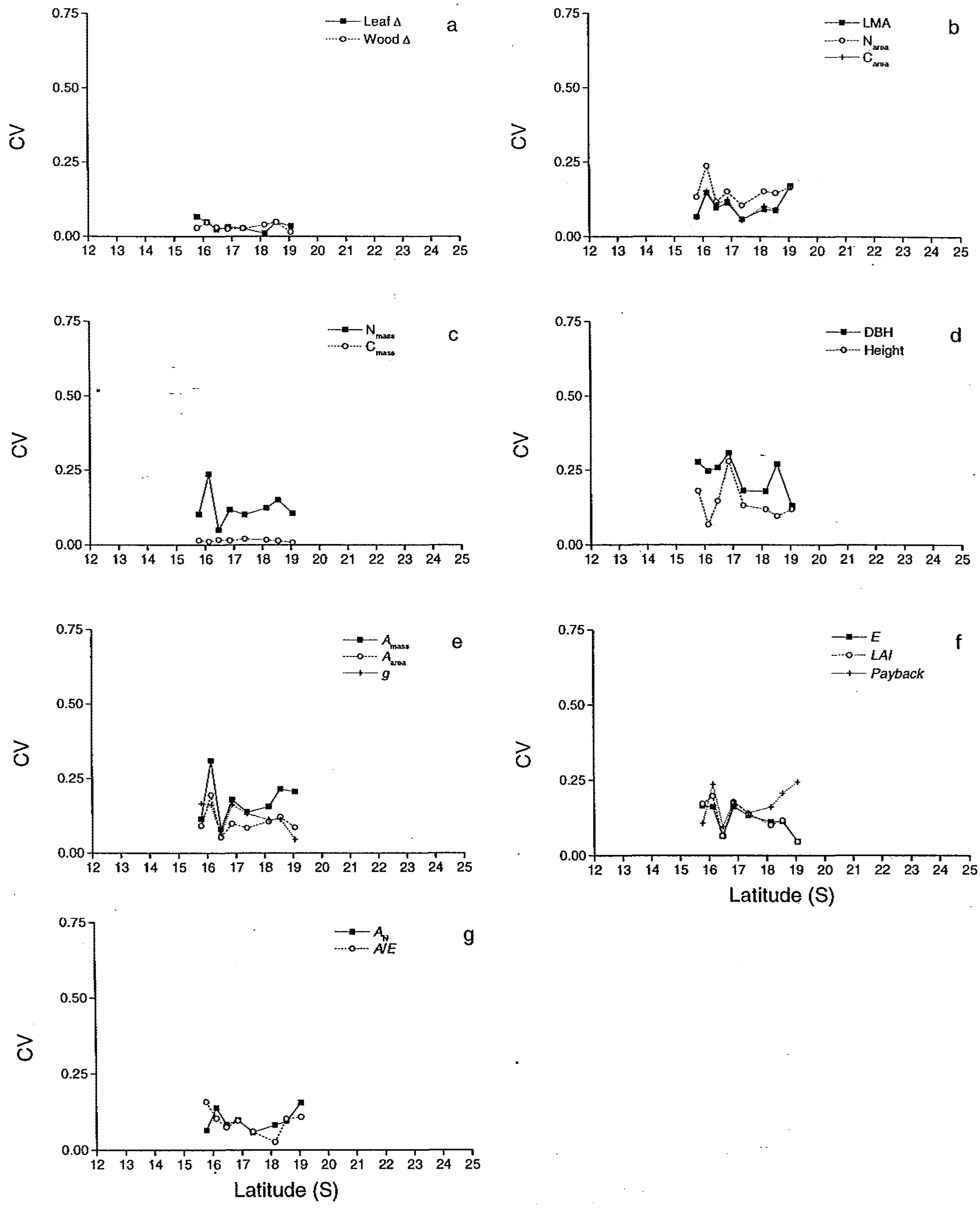


Figure 7.16

E. leucophloia

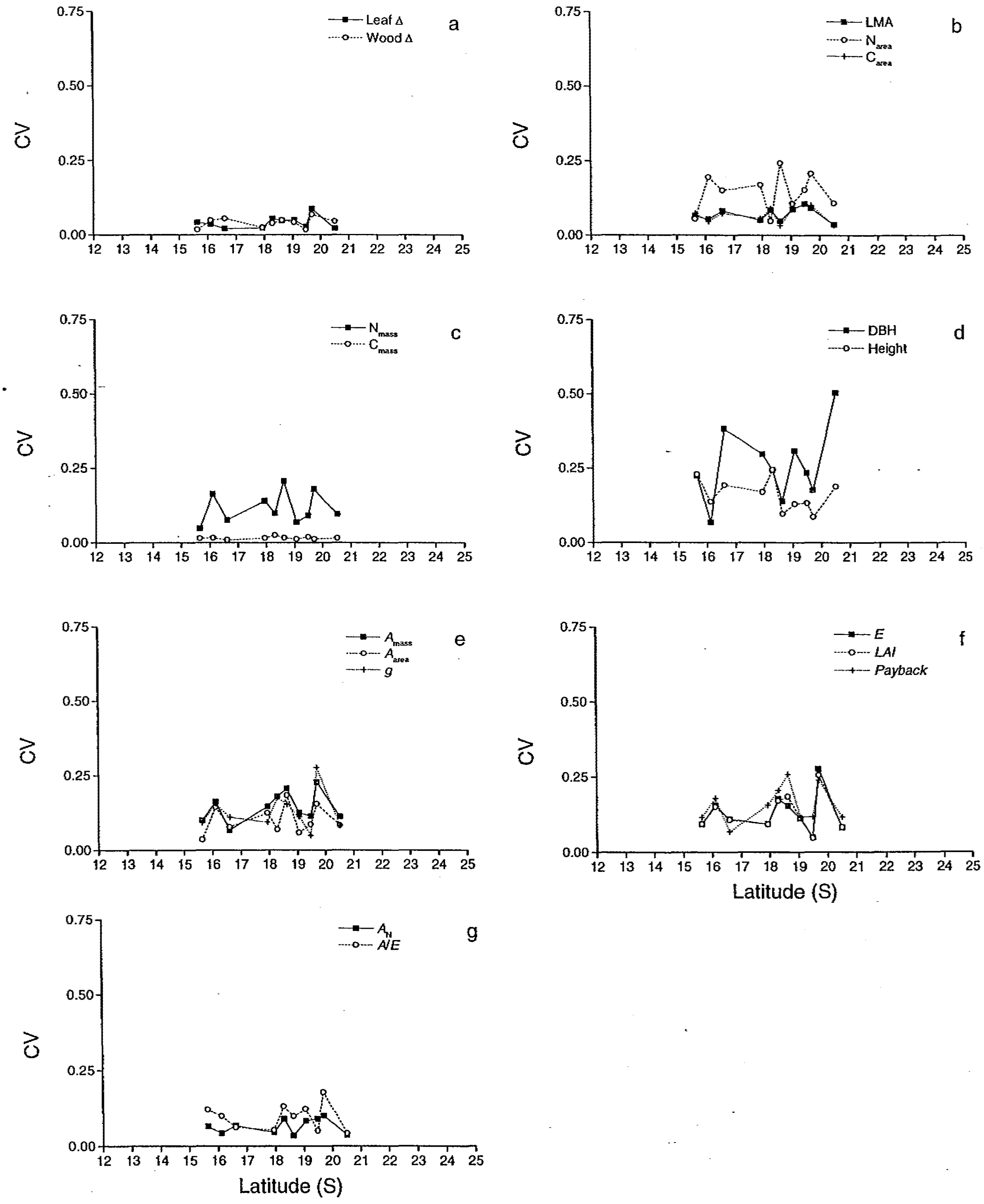


Figure 7.17

E. terminalis

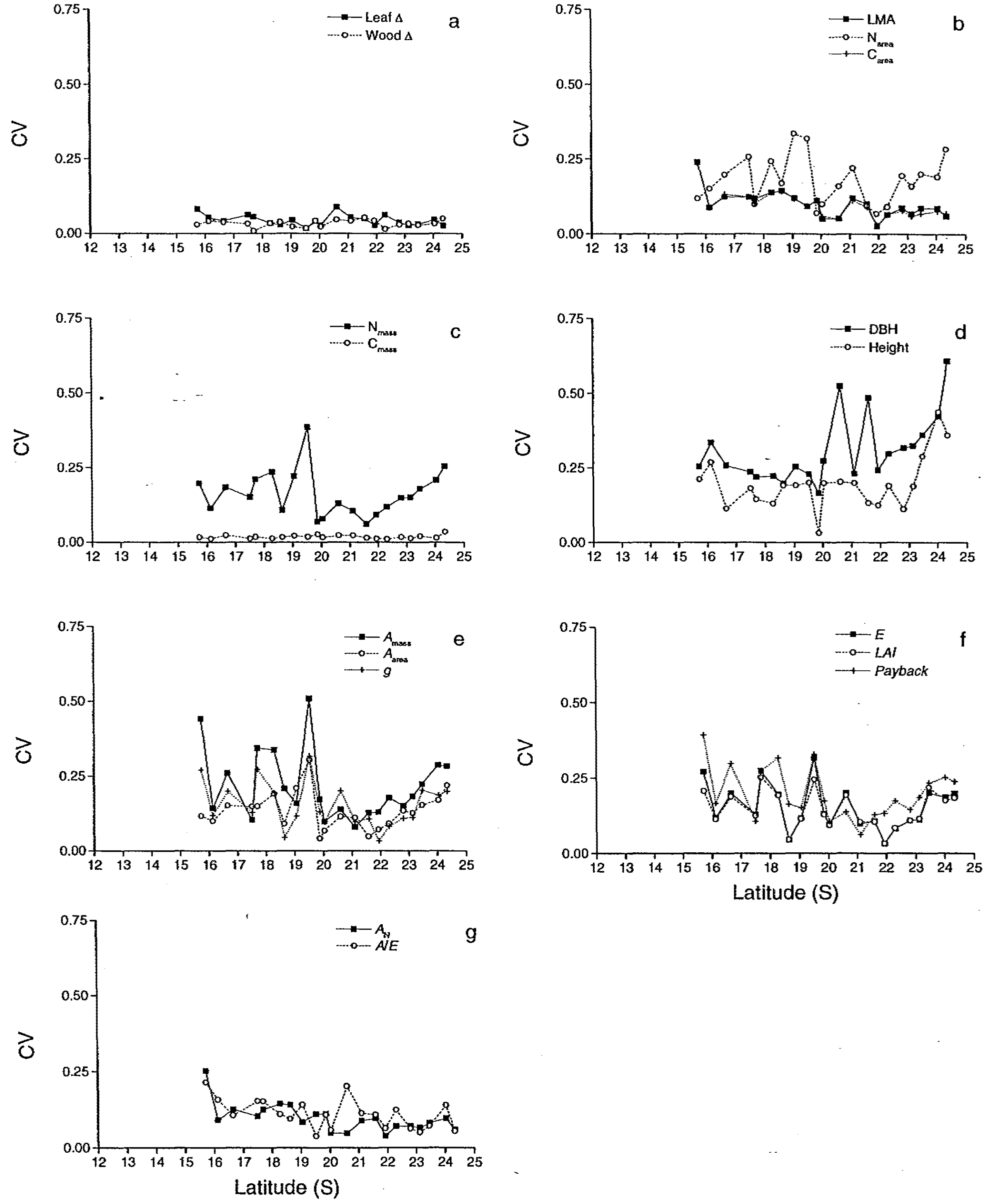


Figure 7.18

E. odontocarpa

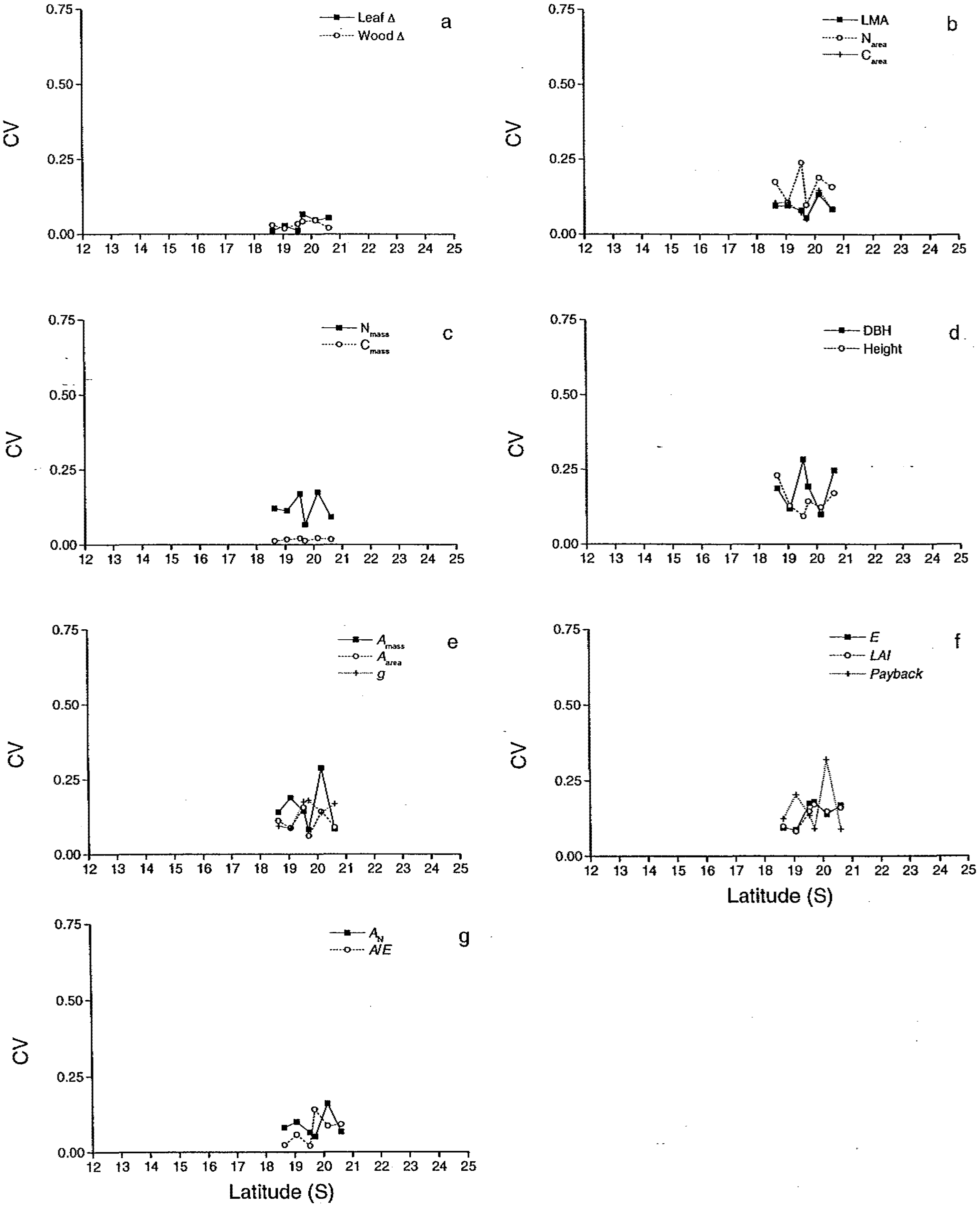


Figure 7.19

E. pachyphylla

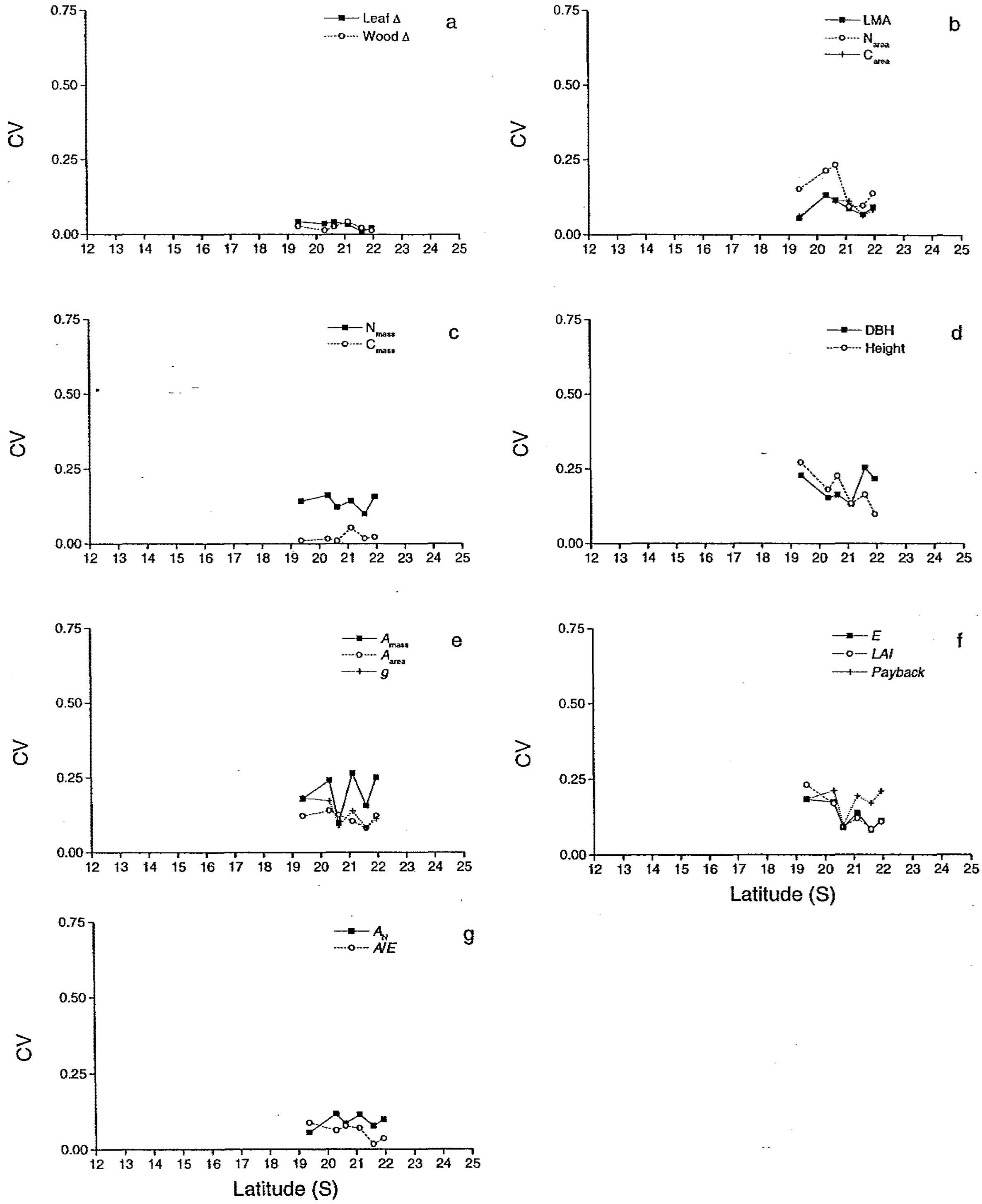


Figure 7.20

E. gamophylla

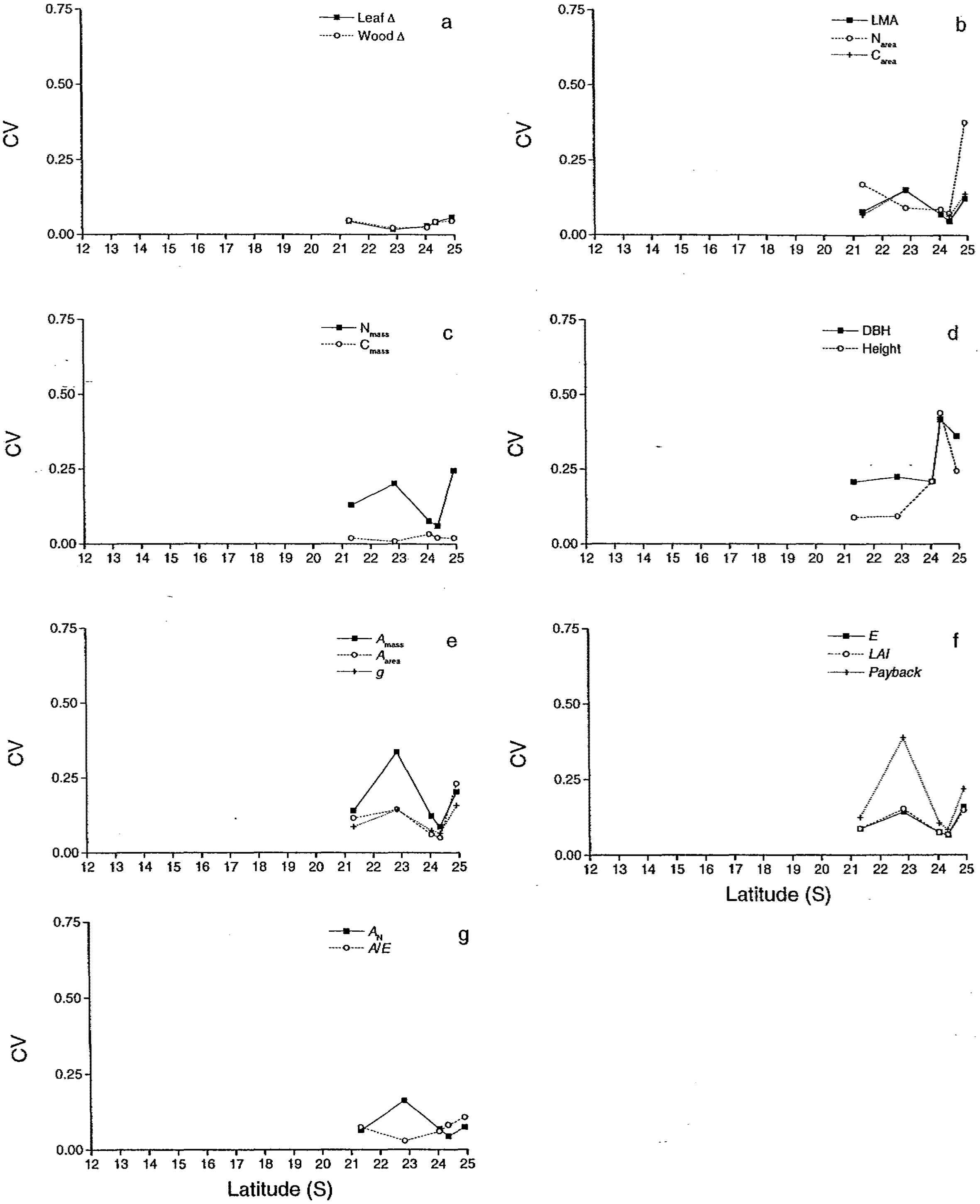


Figure 7.21

8 General discussion and conclusions

The patterns of carbon isotope discrimination in a series of co-occurring and replacement overstory *Eucalyptus* species indicate water availability may be important in determining the limits to the distributions of the species. There was a decrease in Δ with decreasing mean annual rainfall reflecting lower leaf conductances relative to photosynthetic capacities. This indication of increasing stomatal limitation on photosynthesis may imply that the arid boundaries of the distributions of the species are due to an inability to maintain a positive carbon balance. However, the patterns in Δ were not as conclusive as hypothesized, and it would seem that the ability of the species to modify morphological characters, such as leaf area index and leaf payback period, are probably more important than stomatal limitation on carbon gain due to water stress in determining the limits to the distributions of the species. The plasticity of the trees morphological characters probably reduces the physiological strain, and serves to maintain leaf conductances relative to photosynthetic CO_2 assimilation rates and therefore reduce the trends in Δ.

The area-based leaf nitrogen contents increased with decreasing mean annual rainfall. This would be expected according to economic theories describing the resource use of optimal production of firms, since the two resources, water and nitrogen, are substitutable. Econometric modeling showed that the increase in leaf nitrogen contents allowed a significant savings in water-use. All across the gradient in water availability the simulated total canopy assimilation was more sensitive to changes in total canopy nitrogen content that to total canopy transpiration rate. Nitrogen was most strongly limiting total canopy assimilation at the wetter end of the transect.

The increase in leaf nitrogen content with decreasing total annual rainfall was predicted to lead to increases in photosynthetic capacities. The increases in leaf mass per unit area with decreasing total annual rainfall exceeded the changes in predicted assimilation capacity, leading to increasing leaf payback periods. The patterns of leaf payback period presented the strongest evidence as to the mechanism tying decreasing water availability to the distributions of the species.

Since Δ measures the ratio of leaf conductance (g) to assimilation rate (A), patterns in Δ can arise from changes in either g or A. With the available methods, Δ was not found to reflect A, and was therefore more closely related to g and the environmental parameters which could influence g. There were strong co-variances between most of the predicted long-term mean climatic parameters, and none responded as linearly to increasing latitude from north to south as did Δ. Besides measures of total annual rainfall, and rainfall during sub-seasons within the year, carbon isotope discrimination correlated with the patterns in evaporative demands across the transect and with the mean drought lengths (time intervals between rain events).

Plants probably respond to a spatial gradient in water availability differently than to a temporal gradient in water availability. As conditions in time become increasingly stressful, plants either have to decrease their leaf area index or close their stomata as water supply struggles to keep up with evaporative demand. Plants undergo clear physiological strain as a result of the applied environmental strain. Along a spatial gradient it would not be efficient for plants to develop a leaf area index that the water supply could not then support. Along a spatial gradient plants could be expected to grow to a size such that they were all equally constrained by the environmental conditions. As such, it is not surprising that there were not the striking and consistent patterns in leaf and wood Δ revealing increasing periods of water stress across the distributions of the sampled *Eucalyptus* species in the Northern Territory.

Species replacements were not always marked by an obviously greater ability to acquire water and therefore maintain higher leaf conductances relative to assimilation rates. Replacement species did not consistently have higher Δ than species at the arid edge of their distributions. Having a presumed growth strategy allowing increased allocation to root growth did not mean xeric species tending towards extravagant water use where they co-occurred with mesic species. Instead, both species tended to exhibit similar physiological behavior in Δ values. With a further decrease in water availability the xeric species was able to endure even lower long-term average intercellular CO_2 concentrations, while the mesic species dropped out of the community.

The dynamics of the responses of the *Eucalyptus* species to the within year temporal gradient in water availability, i.e. the increasing length of the dry season across the gradient, were not well addressed by single measures of Δ. Wood Δ values, presumably reflecting the performance of the whole leaf canopy over the full course of the year, did show significant trends across the transect more often than the leaf Δ values did. The consistent differences between leaf and wood Δ values within each species raises the possibility that leaves are primarily constructed from annually accumulated carbon reserves, rather than currently fixed carbon. The differences between the leaf and wood Δ values reflect the differences in the components tissue chemistry, which have different isotope signatures, rather than the temporal dynamics of the isotopic signature in the tissue carbon.

Not having a direct measure of the magnitude of either A or g at even a limited subset of the sampling locations made interpreting the patterns, or lack of patterns, in Δ difficult. Clearly changes in the magnitudes of both fluxes are of equal importance to plant performance as the ratio of the two fluxes. The increasing patterns of area-based leaf nitrogen contents with decreasing total annual rainfall would indicate that photosynthetic rates should generally be increasing, which means leaf conductances would have to be decreasing in order to account for the observed patterns in Δ. It would have greatly aided the understanding of the role of water availability in determining the distributions of the selected overstory *Eucalyptus* species to have been able to confirm these predicted patterns of gas exchange.

Predicted long-term mean climate data could not explain much of the variability in Δ data. Rainfall, the evaporative demand, and the period between rain events usually showed higher correlation with Δ values than did leaf nitrogen contents. This would seem to indicate that patterns in Δ were determined by variation in leaf conductances more than they were by assimilation rates. The elasticity of Δ across the distribution of the species was lower than the measured morphological characters, indicating that subtle shifts in Δ may have significant effect on plant performance. The non-linear response of the $A : c_i$ relationship also means there would be a non-linear response between Δ and the magnitude of A and g. A decrease in g, when both g and Δ are high, would cause in a large decrease in Δ but could reflect little decrease in A, while the same decrease in g, when both g and Δ are low, would cause in a smaller decrease in Δ but reflect a large decrease in A. This corresponds to the fact that a decrease in c_i at high c_i causes less of a decrease in A than the same decrease in c_i and low c_i.

Although Δ has the promise of being a quick, efficient method to survey plant gas exchange characteristics at large, continental scales, the realities of the delays in analyzing the samples reduces the applicability in time limited projects. It is clear that no single technique can compensate for a lack of actual time in the field.